A Survey of the Parasites of Freshwater Fishes from the Mainland of British Columbia[1,2]

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ABSTRACT

Examination of 5,456 fish of 36 different species during 1951 and 1952 showed 4,925 or 90 per cent to be infected with at least one species of parasite. Records include fish from many lakes and streams of the Columbia and Fraser drainages and from a few localities in the Skeena, Peace, Liard and Skagit drainages. Parasites are recorded for each species of fish from each locality. The incidence of parasitism in the fish was comparable with that found by other surveys in eastern Canada and the United States. No major differences were found in the parasite faunas of the different river systems. Most of the common parasites were forms of circumpolar or general North American distribution. Several species of parasites described only from the Pacific coast area were common in certain hosts. Introduced species of fish showed very light infections with but few species of their normal parasites. The parasite fauna of fishes of this area appears to be less varied than in eastern and southern parts of the continent.

INTRODUCTION

The parasite fauna of the freshwater fishes of eastern and central North America is fairly well known as the result of several regional surveys and many records of individual parasites. The situation in the western part of the continent has been quite different. Isolated records of parasites from economically important fish and descriptions of a few new species give a very incomplete picture of parasitism in the west. Among those who have contributed to the western records of fish parasitism are: Wardle (1932, 1933a, 1933b), Smedley (1933), Kuitunen-Ekbaum (1933a, 1933b), Lynch (1936), Shaw (1947), Gustafson (1949) and Van Cleave and Lynch (1950). Recently Haderlie (1953) published a fairly extensive study on the parasites of freshwater fishes in Northern California. Our report is unique in the extent of the area from which specimens were obtained and in being the first attempt to give a comprehensive picture of the geographic distribution and of the degree of parasitism in freshwater fishes of this area.

British Columbia comprises an area of 372,630 square miles, stretching from the border of the United States in the south to the Yukon and Alaska in the north and from the Rocky Mountains in the east to the Pacific Ocean. In this area there are five major drainage systems. The headwaters of the Columbia River drain the southeast portion of the Province, while the Fraser arises in the central portion, reaching the sea in the southwest. In the north the Skeena

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flows to the west, and the Peace and Liard with their tributaries, drain the flat prairie land of the north and east towards the Arctic Ocean. Lesser drainages represented are the Skagit River in the south central area and the Yukon in the northwest. These systems include numerous lakes, many of large size.

Our sampling of this large area has been very incomplete, particularly in the north. Systematic collection from Vancouver Island and the many small coastal streams and lakes has not been possible. Most of our material has come from the Columbia and Fraser systems, with only a few collections from the Skeena and Peace drainages. The results indicate, however, that our sample is probably representative of the whole northwest portion of the continent.

The study was initiated in the summer of 1952 and continued through the summer and academic year of 1953–54. Parasites were collected by the investigators in the field during the summer months. Additional examinations of preserved fish were made during the winter of 1953–54 by Bangham who had a research leave from the College of Wooster.

During the first season we were attached to lake survey parties of the British Columbia Game Commission. Their seine hauls and gill-net sets provided specimens for the parasite study. The activities of the first field party with which we worked were centered in the East Kootenay area. Starting at Christina Lake, near Grand Forks, specimens from several lakes in the Kettle River drainage were obtained. Other collections were made in the vicinity of Cranbrook from lakes and streams of the Kootenay system, and finally a single collection was made near Invermere from the headwaters of the Columbia River.

In the middle of July we joined another lake survey party at Prince Rupert. Several lakes draining directly into the sea were sampled in this area. Specimens from Lakelse Lake, near Terrace, and Kathlyn Lake, near Smithers, provided material from the Skeena drainage. Moving farther inland we entered the upper Fraser drainage area. Here extensive collections were obtained from Eulatazella, Cluculz, Nadsilnich (West), and Ness lakes, in the vicinity of Prince George. A trip northeast over the John Hart Highway provided material from the Peace River drainage with collections from Charlie and Azouzetta lakes and also from Pine River and Swamp Creek. Moving southward down the Fraser Valley, collections were made at Dragon Lake near Quesnel, and from Chimney Lake near the town of Williams Lake, where field collecting ended for the season.

During the summer of 1953 our activities were mainly centred in the Okanagan Valley and Kamloops areas. Here we did much of our own collecting, with aid from the Game Department biologists and game wardens. Fish were collected by means of gill netting, seining, and by line fishing in the lakes. Stream fish were usually taken by the use of Fish-tox, a rotenone poison. Some sports fishermen cooperated by allowing us to clean and examine their fish. Collections were made from the Similkameen drainage near Princeton and Keremeos and from large and small lakes and streams in the Okanagan Valley from Osoyoos to Vernon. These included both low-lying lakes and others at higher altitudes in the mountains flanking the valley. The latter part of the season took us over the divide and provided material from the North and South Thompson drainages in the vicinity of Kamloops.

Preserved fish examined during the winter were to a great extent collected for us by the wardens and fishery biologists of the B.C. Game Commission with the purpose of providing samples from areas which we had not personally visited. Thus we had additional fish from Kootenay Lake and some streams near Nelson, from Canim Lake on the Caribou Plateau, from Jackfish Creek on the Alaska Highway and from lakes and streams in the lower Fraser valley below Hope. Some fish collected in previous years and stored by the Game Department were also made available to us. Some of these proved very interesting, especially the material from the Erie chain (pothole, pond, lake, creek) and the specimens of former years from the lakes flowing into Paul Creek. The Fisheries Research Board of Canada provided material from Lakelse Lake and from Port John on the coast near Bella Bella. The Dominion Department of Fisheries collected samples from the Nicola River. Fish from Middle River and Takla Lake in the upper Fraser drainage were provided by the International Salmon Commission. We are indebted to these groups for the assistance they have given in extending our coverage of the area. In particular we wish to acknowledge the generous support of the B.C. Game Commission which helped finance the field and laboratory work and whose personnel under the direction of Dr. P. A. Larkin individually and collectively assisted us greatly. We also wish to acknowledge the contribution to our project made in the grant of a research leave to R. V. Bangham by the Board of Trustees of the College of Wooster for the academic year of 1953–54. Our indebtedness to individuals is acknowledged separately at the end of the paper.

METHODS OF COLLECTION AND STUDY

Whenever possible, fish were examined shortly after collection and the parasites were obtained alive while the fish were fresh. Where facilities for freezing were available, fish frozen overnight or longer yielded well relaxed specimens of parasites, especially gill flukes. After examination of skin, eyes, gills and flesh, the viscera were removed and inspected for gross evidence of parasitism. The intestinal and stomach contents were scraped into Petri dishes. All material from the eyes, gills and gut were examined under wide-field binocular microscopes, the parasites picked out and field indentifications and degree of infection recorded. Contents of the stomach and intestine were then shaken in approximately one per cent sodium bicarbonate solution to loosen the mucous. After settling, decantation of the clear fluid, and one or more washings, the sediment was again examined under the microscope. Parasites were preserved in five per cent formalin after relaxation in water. In the case of Acanthocephala the process of relaxation often required leaving the specimens in water overnight.

Most field identifications were checked from stained whole mounts made during the winters. Delafield's hematoxylin and acetic-alum-carmine were the stains used.

All Gyrodactyloidea were submitted to Dr. John D. Mizelle of Notre Dame University for study and identification to species. The parasitic copepods were referred to Dr. Wilbur M. Tidd of Ohio State University, and one species belonging to the genus *Octomacrum* was sent to Dr. William J. Hargis Jr. of

Florida State University. Their findings have not yet been reported. Dr. Paul V. Gustafson and Dr. James E. Lynch of the University of Washington kindly examined certain parasite species, comparing them with forms they had described for fishes of the Pacific Northwest.

Fish were identified with the aid of descriptions and keys in Carl and Clemens' "The Fresh-water Fishes of British Columbia" (1953). The place names are based on the Geographical Gazetteer of British Columbia.

INCIDENCE AND DIVERSITY OF PARASITISM

The data which follow will show a considerable number of new host records and a great extension of range of certain fish parasites. In addition attention is drawn to three general points of interest: (1) the incidence of parasitism in native fish of this area, (2) the relatively restricted parasite fauna, correlated with a broad host-spectrum of the parasites, and (3) the relatively low incidence of parasitism and absence of normal species of parasites in introduced fish.

Comparison of the incidence and degree of parasitism in British Columbia fishes with those elsewhere in North America is made frequently in the host list which follows. For comparisons with other western regions we have used the findings of Haderlie (1953) in northern California and of Bangham (1951) in the upper Snake River drainage and Yellowstone Lake, Wyoming. In making comparisons with the eastern United States and Canada we have not drawn on the many sources available for those regions but have used only the personal experience of one of us (Bangham). Studies made on the Algonquin Park lakes (Bangham, 1941a; Bangham and Venard, 1946); Lake Huron and Manitoulin Island (Bangham, in press); and the lakes of northern Wisconsin (Bangham, 1946) cover areas at about the same latitude as the regions surveyed in British Columbia. Many of the same species of fish are present in these regions. In the case of some of the warm-water fishes introduced into British Columbia, comparisons have been made with Reelfoot Lake (Bangham and Venard, 1942) and southern Florida (Bangham, 1938). These papers are not cited in detail in the lists but are referred to by locality only.

Of 5,456 fish examined, 4,925 or 90.0 per cent carried at least one species of parasite. A total of 36 species of fish is represented in this group. Somewhat similar incidence of parasitism has been reported for eastern Canada: 1,667 fish of 53 different species from Lake Huron and lakes on Manitoulin Island examined during the summer of 1951 were 98 per cent infected. In lakes of Algonquin Park, Ontario, 79.4 per cent of 1,236 fish belonging to 22 species were parasitized. However, many more *species* of parasites were recorded for the fish of Ontario than for those of British Columbia.

The fish parasites collected in the present survey show more similarity to those taken in the Upper Snake River drainage and from Yellowstone Lake. In this survey 2,535 fish belonging to 14 species showed an infection rate of 92 per cent. Many of the same parasites were found in British Columbia hosts, as might be expected since the Snake River is part of the Columbia River drainage.

The restricted nature of the fish parasite fauna of British Columbia is

especially well illustrated by the endoparasitic flukes, of which only eight species typical of fresh water were recorded, but it is also indicated in other parasite groups. Some species of parasites had a very wide host range and were recovered from a number of different species of fish. This feature is well illustrated by the nematodes and by encysted stages of the trematodes.

Certain forms appear to be restricted to hosts in the Pacific Northwest. Some of the Acanthocephala, a few Cestoda and at least one species of Nematoda belong in this group. Other forms, such as *Neoechinorhynchus rutili*, are found around the world in northern countries and have a wide range of fish hosts (Van Cleave and Lynch, 1950). *Crepidostomum farionis* has been frequently recorded for salmonid fishes in North America as well as in European countries. This fluke was recovered from 12 species of British Columbia fish, being found in largest numbers in the trout and char.

Certain flukes and cestodes appear to be of marine origin and carried by their anadromous hosts into the freshwater habitat. Examples will be given in the discussion by species of fish which follows.

Another noteworthy finding is the very low incidence of parasite occurrence and degree of parasitism in fish which have been introduced into the area by man. Examples such as the catfishes, smallmouth and largemouth bass, yellow perch, sunfish and black crappie all show very few parasites when compared with individuals of the same species from eastern United States and Canada.

GEOGRAPHICAL DISTRIBUTION OF PARASITES

Comparison of the British Columbia findings with similar survey results in other parts of the continent indicate that the parasitic fauna of the fishes of the Pacific northwest is less diversified. Few species are unique for the area. *Neoechinorhynchus venustus* and *N. cristatus* appear to be confined to western North America and are typically parasites of suckers. *Proteocephalus salmonidicola, P. pugetensis,* and *P. ptychocheilus*; *Philonema oncorhynchi, Caryophyllaeus terebrans* and possibly *Rhabdochona cotti* are also western species. None of these, however, was spread as widely through a variety of hosts as were forms of more general North American or circumpolar distribution, e.g. *Neoechinorhynchus rutili, Pomphorhynchus bulbocolli, Crepidostomum farionis, Allocreadium lobatum, Eubothrium salvelini, Hepaticola bakeri, Metabronema salvelini, Rhabdochona cascadilla, Bulbodacnitis globosa* and *Ergasilus caeruleus.* Forms showing least host specificity and highest degree of infection of individual hosts were the encysted larval forms of flukes (*Diplostomulum, Tetracotyle, Neascus* and *Posthodiplostomum minimum*), tapeworms (*Ligula, Diphyllobothrium, Schistocephalus*) and nematodes (*Eustrongylides*). The distribution of these forms is probably dependent mainly on their bird hosts.

In most instances where a parasite was found in some but not all drainage areas of the province the explanation is considered to be that it is host-specific and its normal host is absent from some areas, e.g. *Proteocephalus pinguis* and *Phyllodistomum staffordi.* Three species of parasites, however, show a distribution which cannot be accounted for on this basis. *Caryophyllaeus terebrans,*

Neoechinorhynchus venustus and *N. cristatus* were not obtained from suckers in the Peace River drainage. The Rocky Mountains may have constituted a barrier to the eastward spread of these forms.

British Columbia has emerged comparatively recently from the glacial ice sheet. The time is variously estimated at from 10,000 to 30,000 years. Freshwater fish have established themselves in the province by migration northward through the Columbia and Fraser systems, westward through the Peace and, in the case of salt-tolerant species, from the sea (Carl and Clemens, 1953). At the outset of the study it was anticipated that the distribution of the parasites of the fishes would reflect this history of migration and intrusion into the headwaters of the various river systems.

It may be seen from a map that the collecting sites are to a large extent lakes and streams in the headwaters of the large rivers of the province. In several instances collections from localities separated by relatively short distances belong to quite different watersheds. For example, in the north end of the Okanagan Valley, the Okanagan (Columbia) and South Thompson (Fraser) drainages are represented by several collections. Similarly in the region around Prince George we obtained samples from contiguous portions of the Nechako (Fraser) and Crooked River (Peace) drainages. With relatively little transference of fish in these areas by man as compared with eastern localities, there seems to exist a possibility for checking certain theories concerning the distribution of fish parasites.

However, bearing in mind the incompleteness of our sampling in certain areas, the survey has failed to demonstrate any major differences in parasite fauna in the different drainage systems, or even between the headwaters and lower sections of the same system. The interval of time since the retreat of the ice seems to have been sufficient for most of the parasites to become established throughout the entire area that their hosts have penetrated.

Several species of parasites described from western fishes were not recognized in our material from British Columbia. They are *Proteocephalus tumidocollis* Wagner, 1953, described from *Salmo gairdneri* and *Salvelinus fontinalis* in California; *P. primaverus* Neiland, 1952, reported from *Salmo clarki* in the State of Washington; *Eubothrium oncorhynchi* Wardle, 1932, from *Oncorhynchus* spp. from the Strait of Georgia, B.C.; *Rhabdochona pellucida* Gustafson, 1949, from the squawfish *Ptychocheilus oregonensis* in Washington; *Bulbodacnitis scotti* Simon, 1935, from *Salmo lewisi* in Yellowstone Lake and *B. occidentalis* Smedley, 1933, from *Salmo gairdneri* in British Columbia.

LIST OF PARASITES BY HOST SPECIES AND LOCALITY

An asterisk in front of the name indicates a larval encysted stage, and a double asterisk indicates an immature form within the digestive tract. The number next to a locality is the number of fish examined, whereas the number infected is in brackets following. The number in brackets following each parasite name is the number of hosts in which it was found.

1. Pacific Sea Lamprey. *Entosphenus tridentatus* (Gairdner)

Examined – 10 Infected – 6 Locations – 2

SKEENA DRAINAGE

Lakelse Lake 9(6): °*Eustrongylides* sp. (3), °°*Phyllobothrium* sp. (5).

FRASER DRAINAGE

Nicola River 1(0).

Very few parasites have been recorded from sea lampreys. Both of the parasites found in the lampreys from Lakelse Lake occur in the salmonid fishes. They were probably obtained from such hosts by the feeding of the lampreys.

Nine of 13 sea lampreys, *Petromyzon marinus,* from Lake Huron carried a total of five species of parasites. *Proteocephalus* sp., *Triaenophorus crassus,* and *Diplostomulum* sp. were immature or larval forms and mature *Proteocephalus laruei* and *Echinorhynchus salmonis* were also taken.

Haderlie found no parasites in the eight specimens of pacific lamprey which he examined from northern California.

2. Rocky Mountain Whitefish. *Prosopium williamsoni* (Girard)

Examined – 253 Infected – 213 Locations – 19

COLUMBIA DRAINAGE

Christina Lake 4(4): *Achtheres coregoni* (2), *Bulbodacnitis globosa* (1), *Crepidostomum farionis* (2), *Discocotyle salmonis* (2), *Ergasilus* sp. (1), °*Ligula intestinalis* (1), *Rhabdocona cascadilla* (1), *Salmincola* sp. (1).

Grave Lake 18(15): *B. globosa* (15), °*Diphyllobothrium* sp. (1), *Proteocephalus* sp. (2).

Allison Creek 1(1): *Pomphorhynchus bulbocolli* (1).

Wolfe Creek 8(7): *D. salmonis* (5), *P. bulbocolli* (4).

Okanagan Lake 1(1): °*Diplostomulum* sp. (1), °*Eustrongylides* sp. (1), Gyrodactyloidea (1), *Neoechinorhynchus rutili* (1), *R. cascadilla* (1).

Wood Lake 26(4): °*Diphyllobothrium* sp. (4).

Kootenay Lake 2(1): Gyrodactyloidea (1), *R. cascadilla* (1).

Kettle River 14(7): *Allocreadium lobatum* (3), *Hepaticola bakeri* (4), *Metabronema salvelini* (3), °*Philonema* sp. (1).

FRASER DRAINAGE

Coldwater River 1(1): *A. coregoni* (1), *B. globosa* (1), Gyrodactyloidea (1).

Mabel Lake 5(5): *B. globosa* (1), *C. farionis* (2), °*Diphyllobothrium* sp. (2), *Eubothrium* sp. (1), °*Eustrongylides* sp. (2), *N. rutili* (1), °*Philonema* sp. (1), *Proteocephalus* sp. (1), *R. cascadilla* (2), *Salmincola* sp. (3).

Shuswap Lake (Salmon Arm) 41(41): *A. coregoni* (3), °*Diphyllobothrium* sp. (25), °*Diplostomulum* sp. (4), *D. salmonis* (26), Gyrodactyloidea (30), *M. salvelini* (2), °*Myxosporidia* (2), *N. rutili* (30), °*Philonema* sp. (6), *Proteocephalus exiguus* (12), *R. cascadilla* (5).

Dragon Lake 15(15): *C. farionis* (2), °*Diphyllobothrium* sp. (4), °*Diplostomulum* sp. (15), *P. bulbocolli* (9), *P. exiguus* (14), *R. cascadilla* (1).

Silver Creek 1(1): *R. cascadilla* (1).

Deep Creek (Cluculz Lake) 31(30): *A. coregoni* (7), *C. farionis* (10), *Cystidicola stigmatura* (1), °*Diplostomulum* sp. (16), *Ergasilus* sp. (1), °*Eustrongylides* sp. (3), Gyrodactyloidea (14), *Proteocephalus* sp. (6), *R. cascadilla* (1), °*Tetracotyle* sp. (1).

Cluculz Lake 7(7): *C. farionis* (4), °*Diplostomulum* sp. (5), °*Philonema* sp. (1), *P. exiguus* (5), *R. cascadilla* (2), °*Schistocephalus* sp. (1).

Skeena Drainage

Lakelse Lake 11(8): *C. farionis* (2), °*Diplostomulum* sp. (5), °*Eustrongylides* sp. (3), Gyrodactyloidea (4), *M. salvelini* (1), *P. bulbocolli* (1), *R. cascadilla* (1).

Peace Drainage

Swamp Creek 28(28): Gyrodactyloidea (22), *M. salvelini* (6), *Salmincola* sp. (1).
Pine River 1(1): °*Philonema* sp. (1).

Liard Drainage

Jackfish Creek (Alaska Highway) 36(36): *C. farionis* (36), Gyrodactyloidea (2), *R. cascadilla* (5).

Eight species of parasites were taken from hosts in single locations. *Bulbodacnitis globosa* was found in 15 of 18 hosts at Grave Lake but only in single hosts from three other localities. *Neoechinorhynchus rutili* occurred in 30 of 41 Rocky Mountain Whitefish from Shuswap Lake and in single individuals in two other lakes. *Proteocephalus* sp. appears to be *P. laruei.*

All of 23 Rocky Mountain whitefish from the upper Snake River drainage were infected. A total of nine species of parasites was reported all of which were found in British Columbia whitefish.

3. **Round Whitefish.** *Prosopium cylindraceum quadrilaterale* (Richardson)

Examined – 27 Infected – 27 Locations – 1

Fraser Drainage

Middle River (Takla Lake) 27(27): *Achtheres coregoni* (21), *Bulbodacnitis globosa* (17), *Crepidostomum farionis* (2), °*Cystidicola stigmatura* (8), °*Diplostomulum* sp. (24), °*Eustrongylides* sp. (11), Gyrodactyloidea (25), *Metabronema salvelini* (1), °*Philonema* sp. (12), *Proteocephalus* sp. (2).

Parasites of this fish were in general similar to those from the Rocky Mountain whitefish but the degree of infection was heavier than for those hosts in most locations.

Twenty-two of this host species taken in Lake Huron yielded a total of ten parasite species. Four of the parasites were different from those taken from the Takla Lake individuals. All of eight round whitefish from Opeongo Lake in Algonquin Park carried *Crepidostomum farionis.* Single fish were also infected with *Spinitectus gracilus* and *Ergasilus caeruleus.*

4. **Arctic Grayling.** *Thymallus signifer* (Richardson)

Examined – 1 Infected – 1 Locations – 1

Peace Drainage

Pine River 1(1): *Crepidostomum* sp. (1), *Metabronema* sp. (1).

Only immature stages of these parasites were found. Identification to species has not been possible.

5. **Coho Salmon.** *Oncorhynchus kisutch* (Walbaum)

Examined – 132 Infected – 88 Locations – 7

Coastal Streams

Port John (fry) 8(0), (smolts) 27(24): *Crepidostomum farionis* (6), °*Diphyllobothrium* sp. (1), Gyrodactyloidea (2), *Hepaticola bakeri* (18), *Metabronema salvelini* (1),

Neoechinorhynchus rutili (1), °*Philonema oncorhynchi* (2), °°*Proteocephalus* sp. (2).

SKEENA DRAINAGE

Lakelse Lake (yearlings) 23(22): *C. farionis* (4), °*Diplostomulum* sp. (6), Gyrodactyloidea (9), *M. salvelini* (19), *Pomphorhynchus bulbocolli* (2), *Rhabdocona* sp. (2).
Kathlyn Lake (smolts) 1(1): °*Diplostomulum* sp. (1), *M. salvelini* (1).

FRASER DRAINAGE

Davis Creek (Vernon) (smolts) 10(5): *C. farionis* (1), *N. rutili* (5).
Nicola River (smolts) 1(1): *M. salvelini* (1).
Silver Creek (smolts) 30(7): *M. salvelini* (6), *N. rutili* (1).
Salmon River (smolts) 32(28): *C. farionis* (6), *M. salvelini* (20), *N. rutili* (1), °*P. oncorhynchi* (1).

Haderlie reports taking *Metabronema salvelini, Cystidicola stigmatura, Echinorhynchus lateralis* and *Derogenes* sp. from 1–13 young *O. kisutch* out of 39 examined from northern California coastal streams.

6. **Sockeye Salmon.** *Oncorhynchus nerka* (Walbaum)

Examined – 42 Infected – 33 Locations – 3

COASTAL STREAMS

Prudhomme Lake (adults) 3(3): °*Contracaecum spiculigerum* (2), °*Diphyllobothrium* sp. (1), *Lecithaster salmonis* (1), °Myxosporidia (1), *Philonema oncorhynchi* (3), °°*Phyllobothrium* sp. (2), °°*Proteocephalus* sp. (1), *Rhabdocona cascadilla* (1).
Port John (young fish) 25(16): °*Diphyllobothrium* sp. (14), °*P. oncorhynchi* (1), °°*Proteocephalus* sp. (3).

SKEENA DRAINAGE

Lakelse Lake (adults) 4(4): °*C. spiculigerum* (3), °*Diphyllobothrium* sp. (1), °°Nematode (2), *P. oncorhynchi* (3), °°*Phyllobothrium* sp. (3), *Salmincola* sp. (1).
Lakelse Lake (two-year-olds) 10(10): *Crepidostomum farionis* (1), °*Diphyllobothrium* sp. (1), *Eubothrium* sp. (3), *Metabronema salvelini* (2), °°Nematode (3), *Neoechinorhynchus rutili* (1), °°*Proteocephalus* sp. (6), *Salmincola* sp. (1), °*Tetracotyle* sp. (2).

A marine trematode and a marine cestode were found to be present in the adult fish though these were captured in fresh water. The remaining parasites are similar to the pattern exhibited by the trout. Immature specimens of *Philonema oncorhynchi* were present in the young fish not yet gone to sea, while the adult fish returning from salt water carried mature specimens.

7. **Kokanee.** *Oncorhynchus nerka kennerlyi* (Suckley)

Examined – 87 Infected – 86 Locations – 6

FRASER DRAINAGE

Redfish Creek (Eulatazella Lake) 25(25): °*Diphyllobothrium* sp. (3), *Ergasilus caeruleus* (25), *Neoechinorhynchus rutili* (4), °*Philonema oncorhynchi* (5), *Proteocephalus* sp. (17), °*Schistocephalus* sp. (1).
Cluculz Lake 5(5): *Proteocephalus* sp. (5), *Salmincola* sp. (5).
Takla Lake 17(16): *Crepidostomum farionis* (1), °*Diphyllobothrium* sp. (14), *Metabronema salvelini* (7), *N. rutili* (5), °*P. oncorhynchi* (1), *Proteocephalus* sp. (16).
Shuswap Lake 2(2): °*Diphyllobothrium* (2), *N. rutili* (2), *Proteocephalus exiguus* (2), *Salmincola* sp. (1).

COLUMBIA DRAINAGE

Christina Lake 3(3): *C. farionis* (2), °*Diphyllobothrium* sp. (2), *E. caeruleus* (3), *Proteocephalus* sp. (1).

Goat Creek, Kootenay Lake 35(35): °*Diphyllobothrium* sp. (35), *E. caeruleus* (26), *Eubothrium* sp. (8), *M. salvelini* (8), *N. rutili* (2), °*P. oncorhynchi* (7), *P. exiguus* (35), *Rhabdochona cascadilla* (3).

Diphyllobothrium sp. cysts were frequently taken in fairly large numbers attached to the mesentery near the stomach and pyloric caeca. Most of the *Proteocephalus* sp. appear to be *P. laruei*. The individuals whose gills bore *Ergasilus caeruleus* often had large numbers of these tiny parasitic copepods. Ten kokanee heads with gills were examined from Lac la Hache and there were hundreds of these copepods attached to the outer margins of the gill filaments. These do not appear in our distribution records as only the heads were available for examination.

Haderlie records only *C. farionis* and *Diphyllobothrium* sp. from two California kokanee.

8. **Cut-throat Trout.** *Salmo clarki* Richardson.

Examined – 179 Infected – 178 Locations – 11

Specimens of this fish from the Columbia-Kootenay system are *S. c. lewisi*, Girard, the Yellowstone cut-throat, and from other localities they are probably *S. c. clarki*, the Coastal cut-throat.

COLUMBIA DRAINAGE

Mud (Fish) Creek (Munroe) 11(11): *Crepidostomum farionis* (11).

Joseph Creek (Cranbrook) 18(18): *C. farionis* (17), °*Diplostomulum* sp. (2), *Metabronema salvelini* (13).

Kiakho Lake 20(20): *C. farionis* (19), °*Diphyllobothrium* sp. (14), °*Diplostomulum* sp. (1), *M. salvelini* (2), *Proteocephalus salmonidicola* (17).

Rosen Lake 4(4): *Bulbodacnitis globosa* (2), *C. farionis* (4), °*Diplostomulum* sp. (2), *Hepaticola bakeri* (2), *M. salvelini* (1), *Neoechinorhynchus rutili* (4), *Rhabdochona cascadilla* (1).

COASTAL STREAMS

Prudhomme Lake (Prince Rupert) 10(10): *C. farionis* (1), °*Diphyllobothrium* sp. (5), *H. bakeri* (2), *M. salvelini* (1), °Myxosporidia (kidney) (1), *N. rutili* (10), *P. salmonidicola* (10), *R. cascadilla* (1).

Rainbow Lake 27(27): *C. farionis* (20), °*Diphyllobothrium* sp. (4), *Eubothrium salvelini* (2), °*Eustrongylides* sp. (6), *H. bakeri* (1), *M. salvelini* (10), *N. rutili* (17), °*Philonema oncorhynchi* (1), *P. salmonidicola* (17), *Salmincola edwardsi* (7).

Oliver Lake 10(10): *C. farionis* (2), *M. salvelini* (2), *N. rutili* (8), °*P. oncorhynchi* (1).

FRASER DRAINAGE

Kanaka Creek 52 (52): *C. farionis* (19), *M. salvelini* (52), *N. rutili* (3).

Nicola River 1(0).

SKEENA DRAINAGE

Lakelse Lake 22(22): °*Contracaecum* sp. (2), *C. farionis* (21), °*Diphyllobothrium* sp. (7), °*Diplostomulum* sp. (8), *E. salvelini* (1), °*Eustrongylides* sp. (2), Gyrodactyloidea (8), *H. bakeri* (6), *M. salvelini* (21), °*Neascus* sp. (1), *N. rutili* (16), °*P. oncorhynchi* (1), *Pomphorhynchus bulbocolli* (1), *P. salmonidicola* (11), *R. cascadilla* (1), *S. edwardsi* (1).

Kathlyn Lake (Smithers) 4(4): *C. farionis* (2), *M. salvelini* (1), *N. rutili* (4), *P. bulbocolli* (1), *P. salmonidicola* (3), *S. edwardsi* (1).

The principal parasites of British Columbia cut-throats are *Crepidostomum farionis* (found in 64 per cent of hosts), *Metabronema salvelini* (57 per cent), *Proteocephalus salmonidicola* (32 per cent) and *Neoechinorhynchus rutili* (35 per cent). The most varied infestation occurred at Lakelse Lake, where 22 trout had 16 of 18 species of parasites encountered in the province.

Elsewhere, 9 of the parasites of British Columbia cut-throats were included among 15 species from 291 specimens taken in the Yellowstone-Snake survey. *Bulbodacnitis globosa* was a dominant form there, whereas in British Columbia it was taken only at Rosen Lake. Twelve California cut-throats yielded only *C. farionis, Cystidicola stigmatura* and *Echinorhynchus lateralis,* the latter being an acanthocephalan not taken in any British Columbia fish.

9. **Kamloops Trout.** *Salmo gairdneri kamloops* Jordan

Examined – 696 Infected – 605 Locations – 51

Columbia Drainage

Christina Lake 8(7): *Bulbodacnitis globosa* (1), *Crepidostomum farionis* (5), *Cystidicola stigmatura* (1), *Illinobdella* sp. (1), *Metabronema salvelini* (6), *Proteocephalus salmonidicola* (1).

Jewel Lake 23(22): *C. farionis* (22), °*Diphyllobothrium* sp. (1), °*Diplostomulum* sp. (14), *P. salmonidicola* (1).

Wilgress (Loon) Lake 4(1): *C. farionis* (1).

Premier Lake 1(1): *C. farionis* (1), °*Diplostomulum* sp. (1), *Neoechinorhynchus rutili* (1).

Rosen Lake 10(10): *B. globosa* (3), *C. farionis* (9), °*Diplostomulum* sp. (7), *Hepaticola bakeri* (8), *M. salvelini* (1), *N. rutili* (9), *Rhabdochona cascadilla* (1).

North Star Lake 10(10): *C. farionis* (10), *N. rutili* (1), *R. cascadilla* (1).

Surveyors Lake 1(1): *C. farionis* (1).

Grave Lake 4(4): *B. globosa* (4), *C. farionis* (2).

Lillian Lake 15(15): *C. farionis* (15).

Allison Creek 9(9): *B. globosa* (4), *C. farionis* (7), *Eubothrium salvelini* (1), *M. salvelini* (6).

Keremeos Creek 4(2): *C. farionis* (2).

Wolfe Creek 2(2): *B. globosa* (1), *C. farionis* (2), *M. salvelini* (1), *Pomphorhynchus bulbocolli* (2), *Salmincola edwardsi* (1).

Smiths Pothole 1(0).

Okanagan River (Oliver) 1(0).

Okanagan Lake (Summerland) 6(6): *Allocreadium lobatum* (1), *B. globosa* (4), *C. farionis* (1), °*Diphyllobothrium* sp. (4), °*Diplostomulum* sp. (1), *E. salvelini* (5), *M. salvelini* (1), *N. rutili* (4), *P. salmonidicola* (6), *R. cascadilla* (3).

Shingle Creek 25(21): *B. globosa* (12), *C. farionis* (7), *M. salvelini* (4).

Deep Creek (Peachland) 30(26): *B. globosa* (20), °*B. globosa* (1), *P. salmonidicola* (8).

Summerland Hatchery 18(0).

Swalwell Lake 28(28): *C. farionis* (29), °*Diphyllobothrium* sp. (5), *P. salmonidicola* (1).

Wood Lake 7(7): °*Diphyllobothrium* sp. (2), *Ergasilus caeruleus* (7).

Vernon Creek (at Wood Lake) 25(20): *C. farionis* (15), *E. salvelini* (1), *P. salmonidicola* (7).

Oyama Lake 5(5): *C. farionis* (5).

Coldwater Ditch (Vernon) 31(31): *B. globosa* (28), *C. farionis* (6), *M. salvelini* (25), *S. edwardsi* (20).

Vernon Creek (near Okanagan Lake) 1(0).
Deep Creek (Howcar) 23(23): *C. farionis* (15), *S. edwardsi* (9).

FRASER DRAINAGE

Creighton Creek 45(45): *B. globosa* (43), *C. farionis* (3), *M. salvelini* (45), °*Philonema oncorhynchi* (3).
Davis Creek (Stepney) 2(2): *C. farionis* (1), °*P. oncorhynchi* (1).
Sugar Lake 19(19): *B. globosa* (2), *C. farionis* (4), °*Diphyllobothrium* sp. (9), *E. salvelini* (16), *M. salvelini* (2), *N. rutili* (9), °*P. oncorhynchi* (2), *P. salmonidicola* (19), *S. edwardsi* (9).
Campbell Creek (Kamloops) 12(1): *M. salvelini* (1).
Face Lake 5(5): *B. globosa* (5), *C. farionis* (5), °*Diphyllobothrium* sp. (5), *S. edwardsi* (5).
Pringle Creek 44(40): *C. farionis* (29), °*Diplostomulum* sp. (32), *E. salvelini* (2), *N. rutili* (1), *P. salmonidicola* (1).
Paxton Creek 10(4): *C. farionis* (1), *M. salvelini* (3).
Pinantan Lake 40(39): *B. globosa* (15), *C. farionis* (20), °*Diphyllobothrium* sp. (6), °*Diplostomulum* sp. (1), *N. rutili* (20), *R. Cascadilla* (13).
Paul Lake 13(13): *B. globosa* (13), °*B. globosa* (1), *C. farionis* (4), °*Diphyllobothrium* sp. (6), *E. salvelini* (6).
Heffley Creek 14(11): *C. farionis* (11).
Hihium Lake 15(15): °*Diphyllobothrium* sp. (2), *E. salvelini* (15).
Le Jeune 9(9): *B. globosa* (8), *C. farionis* (9), °*Diphyllobothrium* sp. (2), °*Diplostomulum* sp. (4), *N. rutili* (2), *P. salmonidicola* (7), *S. edwardsi* (4).
Ridge Lake 6(6): *B. globosa* (6), °*Diphyllobothrium* sp. (6), °*Diplostomulum* sp. (5), *S. edwardsi* (6).
Shuswap Lake 1(1): °*Diphyllobothrium* sp. (1), *E. salvelini* (1), *P. salmonidicola* (1).
Coldwater River 1(1): *C. farionis* (1), *M. salvelini* (1).
Middle River 25(25): *B. globosa* (5), *C. farionis* (23), °*Diplostomulum* sp. (3), °Glochidia (2), *M. salvelini* (6), *N. rutili* (3), °*P. oncorhynchi* (2), *P. salmonidicola* (2), *S. edwardsi* (6).
Cluculz Lake 32(31): *C. farionis* (15), °*Diplostomulum* sp. (3), *E. caeruleus* (4), *E. salvelini* (1), *N. rutili* (6), *P. bulbocolli* (6), *P. salmonidicola* (18), *S. edwardsi* (7), °*Schistocephalus* sp. (5).
Deep Creek (Cluculz Lake) 17(15): *C. farionis* (10), °*Diplostomulum* sp. (4), *E. caeruleus* (4), Glochidia (5), *N. rutili* (4), °*P. oncorhynchi* (2), *P. salmonidicola* (1), *R. cascadilla* (1), °*Schistocephalus* sp. (2).
Nadsilnich (West) Lake 18(16): *A. lobatum* (1), *C. farionis* (5), °*Diplostomulum* sp. (2), *E. caeruleus* (3), *M. salvelini* (10), *N. rutili* (2), *P. bulbocolli* (1), *P. salmonidicola* (1).
Joseph Creek (Nadsilnich Lake) 20(15): *C. farionis* (12), °*Diplostomulum* sp. (4), *E. caeruleus* (3), *N. rutili* (1), *R. cascadilla* (1).
Dragon Lake 1(1): °*Diphyllobothrium* sp. (1), °*Diplostomulum* sp. (1), *E. caeruleus* (1), *P. bulbocolli* (1).
Chimney Lake 3(3): *C. farionis* (2), *P. salmonidicola* (1).
Williams Lake 4(4): °*Diplostomulum* sp. (4).
Eighty-three-Mile Creek 1(0).

PEACE RIVER DRAINAGE

Azouzetta Lake 13(13): *C. farionis* (13), °*Diphyllobothrium* sp. (6), *S. edwardsi* (5), °*Schistocephalus* sp. (2).
Swamp Creek 24(20): *C. farionis* (5), *M. salvelini* (20), *N. rutili* (2).

Crepidostomum farionis was recovered from 47 per cent of the Kamloops trout examined from 38 of the locations. *Bulbodacnitis globosa* was found in 26 per cent of the hosts in 17 areas. *Salmincola edwardsi* was scattered in occurrence

being taken in 10 per cent of the individuals. The usual location of these copepods was the inner wall of the operculum or the gill bars, but in several instances they were located in the mouth or back of the pectoral fins.

The cestode most often taken was *Proteocephalus salmonidicola* Alexander, 1951, which was often found in fairly large numbers. It was present in 11 per cent of the kamloops trout examined. Two other species described for trout of the Pacific Coast, *P. primaverus* Neiland, 1952, and *P. tumidocollus* Wagner, 1953, were not recognized in the material from British Columbia.

Philonema oncorhynchi was secured from the body cavity of a very few hosts. This form was first described from the body cavities of the sockeye salmon from British Columbia by Kuitunen-Ekbaum (1933a).

Haderlie records the parasites of 91 *Salmo gairdneri* with 55 parasitized in California. The two most abundant forms were *C. farionis* and *P. salmonidicola*. Six other forms which were found in the British Columbia fish were also recorded in the California study. Haderlie also records as common, occasional or rare, eight other species which we did not find in any of the hosts in the present study.

Among the parasites not reported from California hosts but found in the 696 British Columbia fish were: *Eubothrium salvelini* (48), *Neoechinorhynchus rutili* (65), *Pomphorhynchus bulbocolli* (10), *Allocreadium lobatum* (2), *Cystidicola stigmatura* (1), Glochidia (7), *Hepaticola bakeri* (8), *Rhabdochona cascadilla* (20), *Schistocephalus* sp. (9).

10. **Speckled Char** (Eastern Brook Trout). *Salvelinus fontinalis* (Mitchill)

Examined–110 Infected – 94 Locations – 7

Columbia Drainage

Surveyor's Lake 16(16): *Crepidostomum farionis* (16), °*Diplostomulum* sp. (4), *Hepaticola bakeri* (1), *Neoechinorhynchus rutili* (7), *Rhabdochona* sp. (6).

Lillian Lake 20(15): *C. farionis* (15), °*Ligula intestinalis* (1).

Allison Creek 17(17): *Bulbodacnitis* sp. (3), *C. farionis* (5), *Metabronema salvelini* (16), *Rhabdochona* sp. (1).

Keremeos Creek 8(6): *C. farionis* (6).

Erie Creek 24(24): *B. globosa* (13), *C. farionis* (18), °*Diplostomulum* sp. (1), *M. salvelini* (1), °*Neascus* sp. (2).

Shingle Creek 4(2): *B. globosa* (1), *M. salvelini* (1).

Skagit Drainage

Sumallo River 21(14): *C. farionis* (11), *M. salvelini* (6), *N. rutili* (1).

All parasites were of scattered occurrence except for *Crepidostomum farionis* from 64 per cent of the hosts, *Metabronema salvelini* in 22 per cent and *Bulbodacnitis globosa* recovered in 15 per cent of the B.C. hosts. The brook trout is an introduced fish in British Columbia waters and usually has fewer parasites than the native forms.

Haderlie reports on 31 brook trout collected in California and records 30 parasitized, with *C. farionis* abundant and *Diphyllobothrium* sp. rare.

In brook trout from the upper Snake River, 108 or 75 per cent of the 140 examined carried *C. farionis*. One to four hosts were found to have a total of five other parasite species.

11. Dolly Varden Char. *Salvelinus alpinus malma* (Walbaum)

Examined – 51 Infected – 51 Locations – 9

COLUMBIA DRAINAGE

Joseph Creek (Cranbrook Hatchery) 2(2): *Crepidostomum farionis* (2), *Eubothrium salvelini* (1), °*Eustrongylides* sp. (1), *Metabronema salvelini* (1), *Neoechinorhynchus rutili* (1).

COASTAL STREAMS

Prudhomme Lake (Prince Rupert) (west end) 4(4): *Brachyphallus crenatus* (3), *Bucephalopsis ozakii* (3), *C. farionis* (3), *Contracaecum* sp. (1), °*Contracaecum* sp. (3), *E. salvelini* (2), *Lecithaster salmonis* (2), °Myxosporidia (2), °*Neascus* sp. (3), *Phyllobothrium* sp. (3).

Prudhomme Lake (east end) 20(20): *Bulbodacnitis globosa* (1), *C. farionis* (19), °*Contracaecum* sp. (1), °*Diphyllobothrium* sp. (1), °*Diplostomulum* sp. (4), *E. salvelini* (1), *N. rutili* (11), °*Philonema oncorhynchi* (1), *Salmincola edwardsi* (8), °*Tetracotyle* sp. (1).

Rainbow Lake (Prince Rupert) 8(8): *C. farionis* (6), °*Diphyllobothrium* sp. (1), *Discocotyle salmonis* (1), *E. salvelini* (1), *H. bakeri* (1), *N. rutili* (8), *S. edwardsi* (1).

Oliver Lake (Prince Rupert) 10(10): *C. farionis* (3), °*Eustrongylides* sp. (1), °*Neascus* sp. (2), *N. rutili* (9).

SKEENA DRAINAGE

Lakelse Lake 2(2): *B. globosa* (2), *C. farionis* (1), °*Diplostomulum* sp. (1), *E. salvelini* (2), °*Eustrongylides* sp. (1), Gyrodactyloidea (1), *M. salvelini* (1), *N. rutili* (2), *Proteocephalus salmonidicola* (2).

FRASER DRAINAGE

Cluculz Lake 1(1): *E. salvelini* (1), *S. edwardsi* (1).

Mabel Lake 2(2): *E. salvelini* (1), *N. rutili* (2), *P. salmonidicola* (2).

All of the 51 hosts from the nine locations were infected. *Crepidostomum farionis* and *Neoechinorhynchus rutili* were recovered in 69 per cent of the hosts from all but two of the locations. *Eubothrium salvelini* was taken from 20 per cent of the hosts and from all but one of the areas sampled.

At Prudhomme Lake specimens were obtained from both ends of the lake by gill net. The hosts from the west end, near the outlet, carried the following marine species, *Brachyphallus crenatus, Bucephalopsis ozakii, Lecithaster salmonis, Contracaecum* sp. and *Phyllobothrium* sp., the latter two being larval forms. The 20 Dolly Varden trout from the east end of the lake carried a total of 10 species of parasites, all of which appear to be those of freshwater fishes. Nine species of parasites were taken from the two hosts at Lakelse Lake.

12. Great Lakes Char (Lake Trout). *Cristivomer namaycush* (Walbaum)

Examined – 12 Infected – 12 Locations – 1

FRASER DRAINAGE

Cluculz Lake 12(12): *Bothriocephalus* sp. (1), *Eubothrium salvelini* (12), °*Eustrongylides* sp. (1), *Salmincola* sp. (1).

All of the parasites except *Eubothrium salvelini* were obtained from single host fish. This cestode is a very common parasite of lake trout. In Algonquin Park *E. salvelini* was reported for 20 of 22 hosts from seven lakes. Another but

smaller cestode, *Proteocephalus parallacticus* was taken from 21 of these fish with three other species being found in a few hosts. In Lake Huron *E. salvelini* was taken from all 18 lake trout. Four other species of parasites were found, all different from those at Cluculz Lake. At Jackson Hole in the Snake River drainage, 175 of 184 lake trout were infected with parasites. There were 11 species reported with but two hosts having *E. salvelini*. The nematode, *Bulbodacnitis scotti*, and the fluke, *Crepidostomum farionis*, were the only forms frequently encountered in these hosts.

13. **Fine-scaled Sucker** (Northern Sucker). *Catostomus catostomus* (Forster)

Examined – 234 Infected – 207 Locations – 24

Columbia Drainage

Pinaus Lake 1(1): °*Neascus* sp. (1).

Allison Creek 4(4): *Ergasilus caeruleus* (3), Gyrodactyloidea (2), °*Ligula intestinalis* (1), °*Neascus* sp. (1), *Neoechinorhynchus rutili* (1), *Neoechinorhynchus cristatus* (2), *Pomphorhynchus bulbocolli* (2), *Rhabdochona cascadilla* (1).

Okanagan River (Oliver) 11(8): *Caryophyllaeus terebrans* (4), °*Diplostomulum* sp. (1), *E. caeruleus* (1), °°*Eubothrium* sp. (1), °*Neascus* sp. (4), *N. rutili* (2), *Octomacrum lanceatum* (3), *R. cascadilla* (1), *Plagiocirrus* sp. (1).

Tugulnuit Lake 4(4): *N. cristatus* (2), *O. lanceatum* (1), *R. cascadilla* (1), *Triganodistomum attenuatum* (1).

Twin Lake 1(1): *N. cristatus* (1).

Garnet Valley Reservoir 5(5): Gyrodactyloidea (2), *O. lanceatum* (1), °*Posthodiplostomum minimum* (5).

Vernon Creek (near Okanagan Lake) 5(5): °*Diplostomulum* sp. (3), °*Neascus* sp. (1), *N. rutili* (2).

Premier Lake 23(21): *Allocreadium lobatum* (2), °*Diplostomulum* sp. (3), °Myxosporidia (2), °*Neascus* sp. (17), *R. cascadilla* (8).

Surveyor's Lake 3(3): *C. terebrans* (1), °*Diplostomulum* sp. (1), °Myxosporidia (1), °*Neascus* sp. (2), *R. cascadilla* (2).

Grave Lake 17(13): °*L. intestinalis* (5), *O. lanceatum* (8).

Erie Creek 1(1): °*Neascus* sp. (1).

Skeena Drainage

Kathlyn Lake 9(9): *C. terebrans* (3), °*Diplostomulum* sp. (9), *E. caeruleus* (7), °*L. intestinalis* (1), °*Neascus* sp. (1), *O. lanceatum* (2).

Peace Drainage

Azouzetta Lake 9(8): *C. terebrans* (1), °*Diplostomulum* sp. (1), *E. caeruleus* (2), °*L. intestinalis* (1), °*Neascus* sp. (3), °*Schistocephalus* sp. (1).

Swamp Creek 5(1): °*Diplostomulum* sp. (1).

Fraser Drainage

Middle River (Takla Lake) 1(1): *C. terebrans* (1), *N. cristatus* (1).

Cluculz Lake 5(5): °*Diplostomulum* sp. (5), *E. caeruleus* (1), Gyrodactyloidea (1), °*Neascus* sp. (3), *O. lanceatum* (1).

Deep Creek (Cluculz Lake) 11(11): °*Diplostomulum* sp. (1), *E. caeruleus* (1), *Glaridacris catostomi* (1), *Hepaticola bakeri* (1), °Myxosporidia (2), °*Neascus* sp. (1), *N. cristatus* (7), *Pomphorhynchus bulbocolli* (1), *R. cascadilla* (4), *Triganodistomum attenuatum* (1).

Nadsilnich Lake (West Lake) 1(1): °*Diplostomulum* sp. (1), *G. catostomi* (1), *P. bulbocolli* (1).

Creek from Nadsilnich Lake 7(3): °Myxosporidia (1), °*Neascus* sp. (2).

Ness Lake 29(28): *Actinobdella triannulata* (7), *C. terebrans* (14), °*L. intestinalis* (3), °Myxosporidia (3), °*Neascus* sp. (26), *N. rutili* (2), *N. cristatus* (6).

Dragon Lake 14(14): *A. triannulata* (1), *C. terebrans* (3), °*Diplostomulum* sp. (12), *E. caeruleus* (1), *G. catostomi* (1), *N. rutili* (6), *N. cristatus* (4), *O. lanceatum* (2), *P. bulbocolli* (1), °*Tetracotyle* sp. (1).

Chimney Lake 17(17): °*Diplostomulum* sp. (13), °*L. intestinalis* (4), °Myxosporidia (2), °*Neascus* sp. (3), *N. rutili* (1), *O. lanceatum* (4), *P. bulbocolli* (13), °*Tetracotyle* sp. (7).

Eighty-three-Mile Creek 15(13): °*Diplostomulum* sp. (2), °Myxosporidia (2), *O. lanceatum* (10), *R. cascadilla* (2), °*Tetracotyle* sp. (1).

Hammer Lake 36(30): Gyrodactyloidea (19), °Myxosporidia (4), *O. lanceatum* (1), *P. bulbocolli* (28), °*P. minimum* (1).

Caryophyllaeus terebrans was first described from *Catostomus ardens* taken from Heart Lake in the Yellowstone Park area by Linton in 1893. It was later taken from *Ictiobus bulbatus* by Park H. Simer and recorded by Hunter, 1927. This form was secured from 35 of 36 adult *Catostomus fecundus* from the Snake River (Bangham, 1951). The fine-scaled suckers yielded 12 per cent with *C. terebrans* in the present study. The only other member of this family taken from British Columbia hosts was *Glaridacris catostomi*. This species has a wide distribution in North America and has most often been reported from the common white sucker.

Pomphorhynchus bulbocolli was the ancanthocephalan form most often found in the British Columbia hosts. Twenty per cent of the fine-scaled suckers were infected. The monogenetic fluke, *O. lanceatum*, was rather common on the gills of 14 per cent of the fish. In the Lake Huron studies all of 39 fine-scaled suckers were parasitized with a total of 13 different species. Only four were the same as those recorded from certain B.C. hosts. All of 86 fine-scaled suckers examined from Yellowstone Lake had eye flukes, *Diplostomulum* sp. There were four other parasite species in only a few hosts. There is evidence that fine-scaled suckers were a fairly recent introduction into that lake.

Triganodistomum attenuatum was taken from a single host in each of two locations in our survey. This species was first described from the common white sucker from Oneida Lake (Mueller and Van Cleave, 1932). The host from the Okanagan River carried a large number of long flukes which appear to be an undescribed species of the genus *Plagiocirrus*.

14. Coarse-scaled Sucker. *Catostomus macrocheilus* Girard

Examined – 303 Infected – 268 Locations – 27

Columbia Drainage

Pringle Creek 10(2): °*Diplostomulum* sp. (2).

Pinaus Lake 2(2): *Caryophyllaeus terebrans* (1), °*Neascus* sp. (2), *Neoechinorhynchus cristatus* (1), *Neoechinorhynchus venustus* (1).

Vernon Creek (at Okanagan Lake) 10(10): *C. terebrans* (1), °Myxosporidia (1), °*Neascus* sp. (1), *N. cristatus* (10).

Wood Lake 10(10): *C. terebrans* (1), °Myxosporidia (1), *N. cristatus* (10), *N. venustus* (2), *O. lanceatum* (2).

Okanagan Lake (Summerland) 1(1): *C. terebrans* (1), °*Diplostomulum* sp. (1), *N. cristatus* (1), *N. venustus* (1), *Pomphorhynchus bulbocolli* (1), *Rhabdochona cascadilla* (1).

Tugulnuit Lake 15(5): *N. cristatus* (5), *O. lanceatum* (1), *Triganodistomum attenuatum* (4).

Okanagan River (Oliver) 5(5): *C. terebrans* (2), *Ergasilus caeruleus* (1), Gyrodactyloidea (1), °*Ligula intestinalis* (1), *N. cristatus* (3), *N. venustus* (3), *R. cascadilla* (1), *T. attenuatum* (4).

Wolfe Creek 20(19): *C. terebrans* (2), *Glaridacris catostomi* (1), *N. cristatus* (6), *N. venustus* (3), *O. lanceatum* (1), *P. bulbocolli* (4), *R. cascadilla* (17).

Allison Lake 2(2): °*Diplostomulum* sp. (2), *Neoechinorhynchus rutili* (2).

Kootenay Lake 18(18): *C. terebrans* (3), °*Diplostomulum* sp. (15), *G. catostomi* (1), *Hepaticola bakeri* (1), °*L. intestinalis* (1), *N. cristatus* (9), *N. venustus* (5), *R. cascadilla* (2), °*Spiroxys* sp. (1).

Hansen Lake 1(1): °*Diplostomulum* sp. (1), *E. caeruleus* (1), *N. rutili* (1), *Neoechinorhynchus crassus* (1).

Rosen Lake 34(34): *C. terebrans* (1), °*Diplostomulum* sp. (34), *G. catostomi* (2), °Myxosporidia (1), °*Neascus* sp. (8), *N. crassus* (2), *N. cristatus* (23), *N. venustus* (4), °*Tetracotyle* sp. (1).

Skeena Drainage

Lakelse Lake 5(5): *Actinobdella triannulata* (1), *C. terebrans* (2), °*Diplostomulum* sp. (4), *G. catostomi* (1), °*L. intestinalis* (1), °Myxosporidia (2), *N. cristatus* (3), *N. venustus* (1), *P. bulbocolli* (2), *R. cascadilla* (1), *T. attenuatum* (1).

Fraser Drainage

Nadsilnich (West) Lake 12(12): *A. triannulata* (5), *C. terebrans* (8), °*Diplostomulum* sp. (12), °*Eustrongylides* sp. (3), °Myxosporidia (2), *N. cristatus* (6), *N. venustus* (2), *P. bulbocolli* (12), °*Tetracotyle* sp. (3).

Creek from Nadsilnich Lake 12(6): °*Diplostomulum* sp. (2), *G. catostomi* (1), °Myxosporidia (3), *N. rutili* (2).

Cluculz Lake 5(5): *C. terebrans* (1), °*Diplostomulum* sp. (4), *E. caeruleus* (1), °*Eustrongylides* sp. (1), *G. catostomi* (1), *H. bakeri* (1), °*Neascus* sp. (2), *N. cristatus* (2), *N. venustus* (1), *P. bulbocolli* (5), *R. cascadilla* (1).

Deep Creek (Cluculz Lake) 20(20): °*Diplostomulum* sp. (15), *E. caeruleus* (1), °*Eustrongylides* sp. (1), *G. catostomi* (1), *H. bakeri* (1), °Myxosporidia (2), °*Neascus* sp. (10), *N. cristatus* (11), *N. venustus* (5), *P. bulbocolli* (17), *R. cascadilla* (1).

Chimney Lake 15(15): °*Diplostomulum* sp. (6), °*Neascus* sp. (1), *N. cristatus* (15), *N. venustus* (3), *P. bulbocolli* (9).

Creek into Canim Lake 33(30): *E. caeruleus* (8), °*L. intestinalis* (1), °Myxosporidia (1), °*Neascus* sp. (28), *O. lanceatum* (5), *R. cascadilla* (17), °*Spiroxys* sp. (3).

Campbell Creek 16(16): *C. terebrans* (5), °*Diplostomulum* sp. (7), *N. cristatus* (10), *N. venustus* (9).

Mabel Lake 1(1): *A. triannulata* (1), *C. terebrans* (1), *N. cristatus* (1), *N. venustus* (1), *R. cascadilla* (1).

Shumway Lake 3(3): °*Diplostomulum* sp. (1), °Myxosporidia (1), °*Posthodiplostomum minimum* (1).

Trapp Lake 5(1): °*Neascus* sp. (1).

Shuswap Lake (August 1953) 15(14): °*Diplostomulum* sp. (3), *E. caeruleus* (1), *N. cristatus* (10), *N. venustus* (7), *O. lanceatum* (6), *P. bulbocolli* (1), *R. cascadilla* (3).

Shuswap Lake (Salmon Arm) (Sept. 1953) 31(31): *A. triannulata* (1), *C. terebrans* (2), °*Diplostomulum* sp. (19), *E. caeruleus* (1), *G. catostomi* (1), *N. crassus* (1), *N. cristatus* (21), *N. venustus* (16), *O. lanceatum* (9).

Nicola River 1(0).

Hatzic Lake 1(0).

Diplostomulum sp. was found in the eyes of 42 per cent of the coarse-scaled suckers. *Caryophyllaeus terebrans* was taken from hosts in 14 locations and in

10 per cent of the fish examined. *Glaridacris catostomi* was found in hosts at eight locations.

All of the different species of Acanthocephala recorded in our survey of British Columbia fishes were taken from the coarse-scaled suckers. *Neoechinorhynchus cristatus* was secured from 49 per cent of these hosts, *N. venustus* from 21 per cent and *Pomphorhunchus bulbocolli* from 17 per cent. In 1936 J. E. Lynch described *N. cristatus* and *N. venustus* from *C. macrocheilus* in Washington. He also presented measurements and a redescription of *N. crassus* (western variety).

The ectoparasitic fluke *Octomacrum lanceatum* was described for the common sucker and chub sucker by Mueller (1934) in the series of studies on parasites of Oneida Lake fishes. In the British Columbia survey this parasite was found on the gills of 8 per cent of the hosts.

15. **Common White Sucker.** *Catostomus commersoni* (Lacépède)

Examined – 28 Infected – 27 Locations – 1

Peace Drainage

Charlie Lake (Fort St. John) 28(27): °*Diplostomulum* sp. (6), °*Eustrongylides* sp. (2), *Glaridacris catostomi* (15), °Myxosporidia (5), *Pomphorhynchus bulbocolli* (18).

Over 900 common white suckers were taken in one set of gill nets at Charlie Lake, north of Fort St. John, on the Alaska Highway. On account of time limits, only 28 were examined for parasites. Of these, 64.3 per cent carried *Pomphorhynchus bulbocolli* and 54 per cent *Glaridacris catostomi*. The three other parasite species were encysted forms.

In Wisconsin Bangham found 75 of 77 common white suckers, from 15 locations, to be infected with a total of 20 different parasitic forms. Three were the same species as were taken from the British Columbia hosts.

In Lake Huron and Manitoulin Island 152 common white suckers were infected with a total of 18 species of parasites. *Diplostomulum* sp. was carried by 89 per cent, 60 per cent had *P. bulbocolli*, while 34 per cent yielded *G. catostomi*. Several of the other parasites were different from any of those taken from the British Columbia suckers.

16. **Carp.** *Cyprinus carpio* Linnaeus

Examined – 37 Infected – 33 Locations – 7

Columbia Drainage

Otter Creek (Vernon area) 1(1): Gyrodactyloidea (1).
Twin Lake 22(22): *Dactylogyrus extensus* (22), Gyrodactyloidea (4).
Tugulnuit Lake 1(0).
Okanagan River (near Oliver) 10(9): Gyrodactyloidea (9).
Smiths Pothole (Osoyoos) 1(1): *Caryophyllaeus terebrans* (1), *D. extensus* (1), *Rhabdochona cascadilla* (1), *Trichodina* sp. (1).

Fraser Drainage

Shuswap Lake (Salmon Arm) 1(0).
Hatzic Lake 1(0).

Carp are usually free of parasites and those they carry are frequently gill flukes or external forms.

Haderlie examined 71 California carp with 48 infected. *Dactylogyrus extensus* and *Diplostomulum flexicaudum* are listed as common, with *Lernea carassias* being an occasional parasite.

17. **Chub** (Peamouth). *Mylocheilus caurinus* (Richardson)

Examined – 391 Infected – 370 Locations – 23

Columbia Drainage

Five-Mile Lake (Revelstoke) 8(8): *Caryophyllaeus terebrans* (1), °*Diplostomulum* sp. (1), Gyrodactyloidea (2), *Hepaticola bakeri* (1), °Myxosporidia (1), °*Neascus* sp. (7), °*Posthodiplostomum minimum* (7), *Rhabdochona cascadilla* (1).

Pinaus Lake 10(10): *Allocreadium lobatum* (2), *C. terebrans* (7), °*Diplostomulum* sp. (4), *Eubothrium salvelini* (1), °Myxosporidia (1), °*Neascus* sp. (1), *Octomacrum lanceatum* (2), °*P. minimum* (3), *R. cascadilla* (8), °*Tetracotyle* sp. (2).

Vernon Creek (near Okanagan Lake 2(2): °*Neascus* sp. (2).

Wood Lake 24(24): *C. terebrans* (4), *E. salvelini* (12), Gyrodactyloidea (20), °*Ligula intestinalis* (1), °Myxosporidia (5), °*Neascus* sp. (14), *Proteocephalus ptychocheilus* (9), *R. cascadilla* (1).

Okanagan Lake (Summerland) 48(48): *Bulbodacnitis* sp. (1), °*Diplostomulum* sp. (2), *Ergasilus caeruleus* (14), *E. salvelini* (14), Gyrodactyloidea (41), *H. bakeri* (14), °Myxosporidia (14), °*Neascus* sp. (11), *Neoechinorhynchus rutili* (2), *O. lanceatum* (1), *R. cascadilla* (31), °*Tetracotyle* sp. (1).

Vaseaux Lake 9(8): *E. salvelini* (1), Gyrodactyloidea (8), *H. bakeri* (1), °*L. intestinalis* (1), °Myxosporidia (1), *O. lanceatum* (1), °*P. minimum* (1), *R. cascadilla* (7).

Tugulnuit Lake 7(0).

Okanagan River (near Oliver) 3(3): *E. caeruleus* (1), Gyrodactyloidea (1), °Myxosporidia (1), °*Neascus* sp. (3), °*P. minimum* (3), *R. cascadilla* (3).

Smiths Pothole (Osoyoos) 10(10): *E. caeruleus* (2), *E. salvelini* (3), Gyrodactyloidea (8), *H. bakeri* (1), °Myxosporidia (2), *N. rutili* (1), *R. cascadilla* (9).

Wolfe Creek 1(1): °*Diplostomulum* sp. (1).

Wilgress (Loon) Lake 35(26): °*Clinostomum marginatum* (1), *C. terebrans* (2), °*Diplostomulum* sp. (7), Gyrodactyloidea (10), °*L. intestinalis* (1), °*Neascus* sp. (23), °*P. minimum* (1).

Hansen Lake 4(4): °*Diplostomulum* sp. (4), *E. caeruleus* (4), *E. salvelini* (1), *H. bakeri* (1), *N. rutili* (1), °*P. minimum* (1).

Skeena Drainage

Lakelse Lake (fingerlings) 15(11): °*Diplostomulum* sp. (4), *H. bakeri* (1), *O. lanceatum* (4), °*P. minimum* (9).

Lakelse Lake (adults) 16(16): *A. lobatum* (7), *C. terebrans* (1), °*Diplostomulum* sp. (11), Gyrodactyloidea (14), *H. bakeri* (1), °*Neascus* sp. (2), *N. rutili* (3), *O. lanceatum* (1), *Pomphorhynchus bulbocolli* (2), °*P. minimum* (3).

Kathlyn Lake (Smithers) 26(26): *A. lobatum* (3), *C. terebrans* (22), °*Diplostomulum* sp. (25), *E. salvelini* (13), Gyrodactyloidea (7), °*Neascus* sp. (8), *N. rutili* (16), *P. ptychocheilus* (8), *R. cascadilla* (1), °*Tetracotyle* sp. (1).

Fraser Drainage

Middle River (Takla Lake) 30(30): *A. lobatum* (19), *C. terebrans* (2), °*Diplostomulum* sp. (21), *E. caeruleus* (3), °*Eustrongylides* sp. (1), °Glochidia (3), Grodactyloidea (13), *H. bakeri* (17), °*L. intestinalis* (1), *N. rutili* (4), *O. lanceatum* (8), *P. bulbocolli* (3), *P. minimum* (6), *P. ptychocheilus* (1), *R. cascadilla* (1), °*Tetracotyle* sp. (1).

Cluculz Lake 2(2): °*Diplostomulum* sp. (2), *E. salvelini* (1), Gyrodactyloidea (2), °*P. minimum* (2), *P. ptychocheilus* (1).

Deep Creek (Cluculz Lake) 20(20): *A. lobatum* (1), °*Diplostomulum* sp. (18), *E. salvelini* (2), Gyrodactyloidea (18), *H. bakeri* (1), °*Neascus* sp. (4), *O. lanceatum* (1), *P. bulbocolli* (18), °*P. minimum* (7), *P. ptychocheilus* (1), *R. cascadilla* (3).

Nadsilnich (West) Lake 11(11): °*Diplostomulum* sp. (11), *E. salvelini* (6), Gyrodactyloidea (9), °Myxosporidia (1), *N. rutili* (1), *P. bulbocolli* (1), *P. ptychocheilus* (9), *R. cascadilla* (9).

Davis Creek (Vernon) 5(5): °*Neascus* sp. (4), °*P. minimum* (1).

Mabel Lake 8(8): *E. salvelini* (4), Gyrodactyloidea (7), *Neoechinorhynchus cristatus* (1), *N. rutili* (1), °*P. minimum* (2), *P. ptychocheilus* (4), *R. cascadilla* (4).

Shuswap Lake (Salmon Arm) (July 1953) 47(47): °*Diplostomulum* sp. (2), *E. caeruleus* (1), *E. salvelini* (16), Gyrodactyloidea (46), °*L. intestinalis* (1), °Myxosporidia (3), °*Neascus* sp. (5), *N. cristatus* (8), *Neoechinorhynchus venustus* (5), *O. lanceatum* (9), *P. ptychocheilus* (4), *R. cascadilla* (44).

Shuswap Lake (Salmon Arm) (Aug.–Sept. 1953) 49(49): °*Diplostomulum* sp. (8), *E. salvelini* (32), Gyrodactyloidea (25), °*Neascus* sp. (3), *O. lanceatum* (13), *P. ptychocheilus* (1), *R. cascadilla* (42).

Hatzic Lake 1(1): °*P. minimum* (1).

The parasites are listed in the order of their occurrence with percentage of individuals infected following the parasite name: Gyrodactyloidea–59, *Diplostomulum* sp. – 43, *Rhabdochona cascadilla* – 42, *Eubothrium salvelini* – 27, *Neascus* sp. – 22, *Neoechinorhynchus rutili* – 14, *Posthodiplostomum minimum* – 12, *Caryophyllaeus terebrans* – 10, *Proteocephalus ptychocheilus* – 10, *Hepaticola bakeri* – 10, *Allocreadium lobatum* – 8, *Ergasilus caeruleus* – 6, *Pomphorhynchus bulbocolli* – 6.

Often the degree of infection of individual fish was quite high, especially with *N. rutili, E. salvelini, P. ptychocheilus* and *P. bulbocolli.*

18. **Chisel-mouth.** *Acrocheilus alutaceus* Agassiz and Pickering

Examined – 32 Infected – 27 Locations – 3

Columbia Drainage

Okanagan River (Oliver) 24(24): °°Cestodaria (1), *Ergasilus caeruleus* (3), Gyrodactyloidea (6), °*Neascus* sp. (15), °*Philonema* sp. (1), °*Posthodiplostomum minimum* (12), *Rhabdochona cascadilla* (20).

Tugulnuit Lake 7(3): *R. cascadilla* (3).

Wolfe Creek 1(0).

No previous report on parasites of this host has been found. The hosts from the Okanagan River show a parasite distribution pattern similar to other minnows of the region.

19. **Lake Chub.** *Couesius plumbeus greeni* Jordan

Examined – 161 Infected – 160 Locations – 5

Columbia Drainage

Allison Lake (June, 1948) 46(46): °*Diplostomulum* sp. (28), *Ergasilus caeruleus* (4), °°*Eubothrium* sp. (19), Gyrodactyloidea (4), *Hepaticola bakeri* (5), °*Ligula intestinalis* (4), °Myxosporidia (2), °*Neascus* sp. (1), *Neoechinorhynchus rutili* (4),

Octomacrum sp. (25), °*Posthodiplostomum minimum* (24), *Rhabdochona cascadilla* (3).

Allison Lake (Aug. 1948) 42(41): °*Diplostomulum* sp. (13), *E. caeruleus* (7), °°*Eubothrium* sp. (19), Gyrodactyloidea (4), *H. bakeri* (1), °*L. intestinalis* (1), °*Neascus* sp. (2), *N. rutili* (13), *Octomacrum* sp. (18), °*P. minimum* (16), *R. cascadilla* (1), °*Tetracotyle* sp. (4).

Kootenay Lake 16(16): °*Diplostomulum* sp. (8), Gyrodactyloidea (9), *H. bakeri* (1), *Octomacrum* sp. (1), °*P. minimum* (6), *R. cascadilla* (11), °*Tetracotyle* sp. (1).

FRASER DRAINAGE

Middle River (Talka Lake) 36(36): *Allocreadium lobatum* (4), °*Diplostomulum* sp. (33), *E. caeruleus* (1), °Glochidia (1), Gyrodactyloidea (9), *H. bakeri* (1), °Myxosporidia (2), *N. rutili* (10), °*P. minimum* (5), °°*Proteocephalus* sp. (1), *R. cascadilla* (1), °*Tetracotyle* sp. (3).

Eighty-three-Mile Creek 21(21): *A. lobatum* (12), °*Diplostomulum* sp. (9), *E. caeruleus* (1), Gyrodactyloidea (1), °*Hymenolepis* sp. (5), °Nematode (8), °*P. minimum* (7), *R. cascadilla* (3), °*Tetracotyle* sp. (1).

Of the 18 species of parasites taken, over half represented larval or encysted forms. In many cases these fish act as intermediate hosts and final development takes place in fish-eating birds or in other fish hosts. *Hymenolepis* sp. found as cysts in the body cavity probably has a bird as a final host. A similar form was described by Van Cleave and Mueller (1934). Another encysted form of *Hymenolepis* sp. was recovered from two Utah chubs in Jackson Hole area by Bangham (1951).

Several parasites were taken from hosts in all areas. The most frequent with percentage infestions are: *Diplostomulum* sp. – 56, *Posthodiplostomum minimum* – 33, *Eubothrium* sp. – 22, Gyrodactyloidea – 17, *Rhabdochona cascadilla* – 12.

A small species of *Octomacrum* was recovered from 27 per cent of the hosts. All were from the upper Columbia River drainage. This appears to be the same species that was found on the gills of the red-side shiners.

20. **Long-nose Dace.** *Rhinichthys cataractae* (Cuvier & Valenciennes)

Examined – 44 Infected – 27 Locations – 4

COLUMBIA DRAINAGE

Allison Creek (Princeton) 1(1): °*Neascus* sp. (1), °*Posthodiplostomum minimum* (1).

Shingle Creek (Penticton) 19(11): °*Bulbodacnitis* sp. (1), *Bulbodacnitis* sp. (3), *Metabronema salvelini* (4), °Myxosporidia (4).

Deep Creek (Peachland)11(7): Gyrodactyloidea (7).

PEACE DRAINAGE

Swamp Creek 13(8): °*P. minimum* (5), *Rhabdochona cascadilla* (3).

Posthodiplostomum minimum is the only parasite taken from these hosts in more than one location. Long-nose dace frequently have but few parasites. Five long-nose dace from Pleasant Creek on Manitoulin Island carried only *P. minimum*. All but one of 27 long-nose dace from cold streams in the Jackson Hole area had *P. minimum*. Also recovered from fewer of these hosts were: *Neascus* sp., *Rhabdochona cascadilla*, Gyrodactyloidea, *Contracaecum spiculigerum* and *Allocreadium lobatum*.

21. Squawfish. *Ptychocheilus oregonensis* (Richardson)

Examined – 408 Infected – 373 Locations – 32

COLUMBIA DRAINAGE

Five-Mile Lake (Revelstoke) 1(1): *Eubothrium salvelini* (1), °*Neascus* sp. (1), *Neoechinorhynchus rutili* (1), °*Posthodiplostomum minimum* (1).

Pinaus Lake 8(8): *Allocreadium lobatum* (1), °*Diplostomulum* sp. (6), *Ergasilus caeruleus* (3), °*Ligula intestinalis* (1), °*Neascus* sp. (4), °*P. minimum* (1), *Rhabdochona cascadilla* (2).

Vernon Creek (at Okanagan Lake) 22(15): *E. salvelini* (3), °Myxosporidia (1), *N. rutili* (5), °*P. minimum* (1), *Proteocephalus ptychocheilus* (9), *R. cascadilla* (1).

Wood Lake 28(18): °*Diplostomulum* sp. (1), *E. caeruleus* (1), *E. salvelini* (7), °*Neascus* sp. (1), *N. rutili* (3), *P. ptychocheilus* (6), *R. cascadilla* (9).

Okanagan Lake (Summerland) 8(8): *E. salvelini* (2), Gyrodactyloidea (5), °*Neascus* sp. (1), *N. rutili* (5), *P. ptychocheilus* (6), *R. cascadilla* (5), °*Spiroxys* sp. (1).

Vaseaux Lake 2(1): *N. rutili* (1), *P. ptychocheilus* (1), *R. cascadilla* (1).

Tugulnuit Lake 16(9): *E. salvelini* (3), Gyrodactyloidea (1), *N. rutili* (5), *R. cascadilla* (6).

Okanagan River (Oliver) 3(3): Gyrodactyloidea (2), °*Neascus* sp. (2), *N. rutili* (1), °*P. minimum* (3), *R. cascadilla* (3).

Wolfe Creek 18(18): *A. lobatum* (1), °*Diplostomulum* sp. (8), Gyrodactyloidea (15), *Hepaticola bakeri* (1), *Illinobdella* sp. (2), °Myxosporidia (1), °*Neascus* sp. (8), *N. rutili* (4), °*P. minimum* (10), *P. ptychocheilus* (1), *R. cascadilla* (1).

Allison Creek (Princeton) 16(16): *A. lobatum* (3), °*Diplostomulum* sp. (2), *E. salvelini* (10), Gyrodactyloidea (16), °Myxosporidia (1), °*Neascus* sp. (11), *N. rutili* (8), °*P. minimum* (14), *Pomphorhynchus bulbocolli* (14), *P. ptychocheilus* (9), *R. cascadilla* (14).

Allison Lake 2(2): °*Diplostomulum* sp. (1), Gyrodactyloidea (1), °*P. minimum* (2), *P. ptychocheilus* (1), *R. cascadilla* (1).

Outlet of Duck Lake (Kootenay) 2(2): °*Diplostomulum* sp. (2), °*Neascus* sp. (2), *N. rutili* (1), °*P. minimum* (2).

Kootenay Lake 3(3): °*Diplostomulum* sp. (3), Gyrodactyloidea (2), *N. rutili* (1), °*P. minimum* (2), *R. cascadilla* (2), °*Tetracotyle* sp. (1).

Kettle River (South Fork) 1(1): *H. bakeri* (1), °*Neascus* sp. (1), °*P. minimum* (1), *R. cascadilla* (1).

Christina Lake 16(14): *E. caeruleus* (3), Gyrodactyloidea (2), *H. bakeri* (1), *Illinobdella* sp. (1), °Myxosporidia (3), °*Neascus* sp. (2), °*P. minimum* (10), *P. ptychocheilus* (1), *R. cascadilla* (10).

Hansen Lake 15(15): °*Diplostomulum* sp. (15), *E. caeruleus* (15), *E. salvelini* (13), Gyrodactyloidea (1), *H. bakeri* (4), *N. rutili* (15), °*P. minimum* (8), *P. ptychocheilus* (1), *R. cascadilla* (15), °*Tetracotyle* sp. (5).

SKEENA DRAINAGE

Lakelse Lake 17(17): °*Contracaecum spiculigerum* (2), °*Diplostomulum* sp. (9), Gyrodactyloidea (9), *N. rutili* (8), °*P. minimum* (6), *P. bulbocolli* (2), *P. ptychocheilus* (6), °Cestode (1).

Kathlyn Lake (Smithers) 16(16): °*Diplostomulum* sp. (16), *E. salvelini* (8), Gyrodactyloidea (8), °Glochidia (2), °*Neascus* sp. (3), *N. rutili* (13), *P. ptychocheilus* (2), °*Tetracotyle* sp. (13).

FRASER DRAINAGE

Middle River (Takla Lake) 23(23): *A. lobatum* (3), °*Diplostomulum* sp. (14), *E. caeruleus* (2), *E. salvelini* (10), Gyrodactyloidea (15), *H. bakeri* (3), °*L. intestinalis* (1), *N. rutili* (7), °*P. minimum* (5), *P. bulbocolli* (1), *P. ptychocheilus* (15), *R. cascadilla* (8), °*Spiroxys* sp. (1).

Cluculz Lake 19(19): *A. lobatum* (8), °*Diplostomulum* sp. (15), *E. salvelini* (11), Gyrodactyloidea (8), *H. bakeri* (5), °*Neascus* sp. (12), *N. rutili* (2), °*P. minimum* (15), *P. bulbocolli* (2), *P. ptychocheilus* (14), *R. cascadilla* (2).

Deep Creek (Cluculz Lake) 21(21): *A. lobatum* (7), °*Diplostomulum* sp. (17), *E. salvelini* (6), Gyrodactyloidea (6), *H. bakeri* (3), °*Neascus* sp. (19), *N. rutili* (3), °*P. minimum* (21), *P. bulbocolli* (4), *P. ptychocheilus* (6), *R. cascadilla* (15).

Nadsilnich (West) Lake 12(12): °*Diplostomulum* sp. (11), *E. salvelini* (1), Gyrodactyloidea (9), *H. bakeri* (1), °*Neascus* sp. (5), *N. rutili* (4), °*P. minimum* (11), *P. bulbocolli* (3), *P. ptychocheilus* (8), *R. cascadilla* (9), °*Tetracotyle* sp. (1).

Outlet of Nadsilnich Lake 23(21): °*Diplostomulum* sp. (10), *E. caeruleus* (1), *H. bakeri* (1), °*L. intestinalis* (1), °*Neascus* sp. (16), *N. rutili* (2), *R. cascadilla* (11).

Dragon Lake (Quensel) 14(14): °*Diplostomulum* sp. (14), *E. salvelini* (4), *H. bakeri* (7), °*P. minimum* (5), *P. bulbocolli* (3), *P. ptychocheilus* (11), *R. cascadilla* (9), °*Tetracotyle* sp. (8).

Davis Creek 6(2): °*L. intestinalis* (1), °*Neascus* sp. (1), °*P. minimum* (1).

Mabel Lake 6(6): *E. salvelini* (5), Gyrodactyloidea (4), °*Neascus* sp. (1), *N. rutili* (2), °*P. minimum* (3), *P. ptychocheilus* (6), *R. cascadilla* (4).

Shuswap Lake (Salmon Arm) (July 1953) 32(30): °*Diplostomulum* sp. (3), *E. caeruleus* (1), *E. salvelini* (13), Gyrodactyloidea (6), *H. bakeri* (1), °*L. intestinalis* (2), °Myxosporidia (2), *N. rutili* (3), *P. ptychocheilus* (16), *R. cascadilla* (13).

Shuswap Lake (Salmon Arm) (Aug.–Sept. 1953) 28(28): °*Diplostomulum* sp. (14), *E. salvelini* (17), Gyrodactyloidea (13), *H. bakeri* (5), °*L. intestinalis* (1), *N. rutili* (8), *P. ptychocheilus* (17), *R. cascadilla* (7).

Trapp Lake 1(1): °*P. minimum* (1).

Creek into Canim Lake 26(26): °*Diplostomulum* sp. (1), *E. salvelini* (12), Gyrodactyloidea (13), *H. bakeri* (6), °*L. intestinalis* (3), °Myxosporidia (1), °*Neascus* sp. (15), *N. rutili* (1), °*P. minimum* (20), *P. bulbocolli* (6), *R. cascadilla* (21), °*Tetracotyle* sp. (20).

Nicola River 1(1): °*P. minimum* (1), *R. cascadilla* (1).

Hatzic Lake 2(2): °*P. minimum* (2).

In our survey it is rather unusual to find so many different parasites in more than one-third to one-fourth of all hosts. No marked distribution pattern appears in the different river systems. *Proteocephalus ptychocheilus* was first described for this host from Montana (Faust, 1920). This parasite was obtained from 33 per cent of the British Columbia squawfish in 19 locations. *Eubothrium salvelini*, another cestode parasite was recorded for 31 per cent of the hosts from 17 locations.

A small nematode frequently encountered in cyprinid fishes over a wide area of North America, *Rhabdochona cascadilla*, was recovered from 42 per cent of hosts in 25 different areas. Another nematode, *Hepaticola bakeri*, was taken from 9 per cent of the squawfish from 13 locations. The only acanthocephalan forms taken from the squawfish were *Neoechinorhynchus rutili* and *Pomphorhynchus bulbocolli*. The former was recorded from 25 per cent of the hosts from 23 locations. *P. bulbocolli* was found in 8 per cent of squawfish from eight locations.

Encysted eye flukes, *Diplostomulum* sp., were recovered from 40 per cent of the hosts in 19 of the 32 areas where squawfish were taken, while the cysts of the strigeid fluke, *Posthodiplostomum minimum*, were found in 36 per cent of the hosts in 24 locations. Often very heavy infections were present. Another strigeid fluke, *Tetracotyle* sp., was taken from 12 per cent of hosts in seven areas,

while a third species, *Neascus* sp., was found in black pigmented cysts in the skin of 26 per cent of squawfish from 18 locations.

In the 1951 survey of Jackson Hole fish parasites, Bangham reports on the results of examination of 670 Utah chubs, *Gila straria,* a fish occupying the same ecological niche as the squawfish. There were 25 different species of parasites taken from certain of 660 of these hosts. Fourteen species were the same as those obtained from British Columbia squawfish. The forms most frequently encountered in the Snake River Utah chubs were: *P. minimum, R. cascadilla, Clinostomum marginatum, Glaridacris* sp., *N. rutili, Contracaecum spiculigerum* and *Diplostomulum* sp.

Of the species reported by Haderlie from *Ptychocheilus grandis* in California, only *P. minimum* and *Neascus* sp. were found in the squawfish of British Columbia.

22. **Redside Shiner.** *Richardsonius balteatus* (Richardson)

Examined – 1,532 Infected – 1,493 Locations – 45

Columbia Drainage

Premier Lake (Cranbrook) 19(19): *Allocreadium lobatum* (3), °*Diplostomulum* sp. (1), *Ergasilus caeruleus* (1), *Hepaticola bakeri* (2), °*Neascus* sp. (1), *Neoechinorhynchus rutili* (9), *Octomacrum* sp. (2), °*Posthodiplostomum minimum* (19), *Rhabdochona cascadilla* (16).

Rosen Lake 36(36): *A. lobatum* (3), °*Diplostomulum* sp. (35), Gyrodactyloidea (34), °*Ligula intestinalis* (2), °*Neascus* sp. (24), *N. rutili* (31), °*P. minimum* (36), °*Tetracotyle* sp. (7).

Surveyor's Lake 69(68): °*Diplostomulum* sp. (1), Gyrodactyloidea (26), *H. bakeri* (3), °*L. intestinalis* (8), °*Neascus* sp. (20), *N. rutili* (32), *Octomacrum* sp. (12), °*P. minimum* (67), *R. cascadilla* (54).

Kootenay Lake 32(32): *A. lobatum* (3), °*Diplostomulum* sp. (26), Gyrodactyloidea (16), °*L. intestinalis* (1), °Myxosporidia (2), *N. rutili* (15), °*P. minimum* (31), *R. cascadilla* (10).

Erie Pothole 33(33): *A. lobatum* (4), °*Clinostomum marginatum* (12), Gyrodactyloidea (29), *H. bakeri* (1), °*Neascus* sp. (32), *N. rutili* (31), *Octomacrum* sp. (27), °*P. minimum* (33), *R. cascadilla* (1).

Erie Pond 31(31): *A. lobatum* (1), °*C. marginatum* (2), Gyrodactyloidea (1), *H. bakeri* (1), °Myxosporidia (1), °*Neascus* sp. (6), *N. rutili* (27), *Octomacrum* sp. (17), °*P. minimum* (28), *R. cascadilla* (28).

Erie Lake 47(47): *A. lobatum* (1), °*C. marginatum* (2), °°*Eubothrium* sp. (1), Gyrodactyloidea (5), °*L. intestinalis* (4), °*Neascus sp.* (26), *N. rutili* (42), *Octomacrum* sp. (17), °*P. minimum* (46), *R. cascadilla* (32), °*Tetracotyle* sp. (1).

Erie Creek 3(3): *H. bakeri* (1), °Myxosporidia (2), °*Neascus* sp. (2), *N. rutili* (3), *Octomacrum* sp. (1), °*P. minimum* (2), *R. cascadilla* (2).

Allison Creek (Princeton) 7(7): °*Diplostomulum* sp. (1), °°*Eubothrium* sp. (1), Gyrodactyloidea (4), °*Neascus* sp. (3), *N. rutili* (2), °*P. minimum* (3), *R. cascadilla* (7).

Wolfe Creek (Princeton) 24(24): *A. lobatum* (4), *Bulbodacnitis* sp. (1), °*Diplostomulum* sp. (1), Gyrodactyloidea (4), *H. bakeri* (3), °*Neascus* sp. (1), *N. rutili* (5), *Pomphorhynchus bulbocolli* (18), °*P. minimum* (2), *R. cascadilla* (7).

Dry Lake (Princeton) 1(1): °*Diplostomulum* sp. (1), Gyrodactyloidea (1), °*P. minimum* (1).

Laird Lake (Princeton) 45(45): °*Diplostomulum* sp. (24), *E. caeruleus* (1), Gyrodactyloidea (33), °Myxosporidia (10), °*Neascus* sp. (43), *N. rutili* (32), *Octomacrum* sp. (2), *P. bulbocolli* (39), °*P. minimum* (41), *R. cascadilla* (24).

Smiths Pothole (Osoyoos) 1(1): Gyrodactyloidea (1), *N. rutili* (1), °*P. minimum* (1).

Okanagan River (Oliver) 27(27): °°*Eubothrium* sp. (1), Gyrodactyloidea (22), °*Neascus* sp. (10), °*P. minimum* (14), *R. cascadilla* (23).

Tugulnuit Lake 2(2): *R. cascadilla* (2).

Vaseaux Lake 6(6): °*Diplostomulum* sp. (1), Gyrodactyloidea (6), °Myxosporidia (2), *N. rutili* (4), *R. cascadilla* (2).

Okanagan Lake (Summerland) 22(22): *E. caeruleus* (2), Gyrodactyloidea (11), °*Neascus* sp. (8), *N. rutili* (19), °*P. minimum* (3), *R. cascadilla* (12).

Garnet Valley Reservoir 36(36): °°*Eubothrium* sp. (1), Gyrodactyloidea (34), °*Neascus* sp. (10), *N. rutili* (31), °*P. minimum* (36), °°*Proteocephalus* sp. (1).

Otter Creek (Vernon) 21(21): °Glochidia (1), Gyrodactyloidea (4), °Myxosporidia (1), °*Neascus* sp. (11), °*P. minimum* (20), *R. cascadilla* (2).

Vernon Creek (near Okanagan Lake) 32(30): *E. caeruleus* (4), °°*Eubothrium* sp. (1), Gyrodactyloidea (13), °*L. intestinalis* (1), °*Neascus* sp. (7), *N. rutili* (24), °*P. minimum* (6), °°*Proteocephalus* sp. (1), *R. cascadilla* (21).

Goose Lake Irrigation Ditch (Kootenay Lake) 24(18): °*Diplostomulum* sp. (2), °*P. minimum* (17), *R. cascadilla* (2).

Allison Lake 34(34): °*Diplostomulum* sp. (7), *E. caeruleus* (6), °°*Eubothrium* sp. (7), Gyrodactyloidea (22), °*L. intestinalis* (13), °*Neascus* sp. (3), *N. rutili* (33), °*P. minimum* (6).

Borgeson Lake 14(14): °*Diplostomulum* sp. (5), Gyrodactyloidea (1), °*Neascus* sp. (13), *N. rutili* (10), *P. bulbocolli* (8), °*P. minimum* (14), *R. cascadilla* (1).

Fraser Drainage

Middle River (Takla Lake) 108(108): *A. lobatum* (13), °*C. marginatum* (2), °*Diplostomulum* sp. (71), *E. caeruleus* (16), Gyrodactyloidea (104), *H. bakeri* (18), °Myxosporidia (1), °*Neascus* sp. (2), *N. rutili* (95), *Octomacrum* sp. (13), °*P. minimum* (3), *R. cascadilla* (24).

Nadsilnich (West) Lake 1(1): °*Diplostomulum* sp. (1), Gyrodactyloidea (1), °*L. intestinalis* (1), °*Neascus* sp. (1), *N. rutili* (1), °*Tetracotyle* sp. (1).

Creek from Nadsilnich Lake 33(30): °*Diplostomulum* sp. (23), *H. bakeri* (4), °Myxosporidia (1), °*Neascus* sp. (18), *N. rutili* (17), °*P. minimum* (6), *R. cascadilla* (14).

Deep Creek (Cluculz Lake) 38(38): *A. lobatum* (3), °*Diplostomulum* sp. (28), *E. caeruleus* (5), °°*Eubothrium* sp. (4), Gyrodactyloidea (12), *H. bakeri* (4), °*Neascus* sp. (37), *N. rutili* (28), *Octomacrum* sp. (1), *P. bulbocolli* (1), °*P. minimum* (9), *R. cascadilla* (23).

Chimney Lake (near Williams Lake) 13(13): °*Diplostomulum* sp. (6), Gyrodactyloidea (13), °*Neascus* sp. (6), *N. rutili* (13), *P. bulbocolli* (6), °*Tetracotyle* sp. (3).

Williams Lake 1(1): °*Neascus* sp. (1), *P. bulbocolli* (1), *R. cascadilla* (1).

Marquart Lake 15(6): Gyrodactyloidea (skin) (1), Gyrodactyloidea (gills) (3), °*Neascus* sp. (2), *R. cascadilla* (1).

Courtney Lake 32(32): °*Diplostomulum* sp. (13), Gyrodactyloidea (30), °*L. intestinalis* (8), °*Neascus* sp. (32), *Octomacrum* sp. (1), °*P. minimum* (32), *R. cascadilla* (3), °*Tetracotyle* sp. (19).

Nicola River 1(1): Gyrodactyloidea (1).

Campbell Creek 54(51): °*Diplostomulum* sp. (13), Gyrodactyloidea (7), °*Neascus* sp. (1), *N. rutili* (30), °*P. minimum* (50), *R. cascadilla* (3).

Davis Creek 34(34): °°*Eubothrium* sp. (2), Gyrodactyloidea (34), *H. bakeri* (1), °*Neascus* sp. (32), *N. rutili* (15), °*P. minimum* (21), *R. cascadilla* (15).

Trapp Lake 34(34): *E. caeruleus* (10), Gyrodactyloidea (22), °*L. intestinalis* (1), °Myxosporidia (2), °*Neascus* sp. (1), *N. rutili* (24), °*P. minimum* (33), *R. cascadilla* (1).

Shumway Lake 14(14): °*Diplostomulum* sp. (4), °Myxosporidia (1), °*Neascus* sp. (2), *N. rutili* (14), °*P. minimum* (9).

Pringle Creek 6(6): Gyrodactyloidea (6), °*L. intestinalis* (1), °Myxosporidia (1), °*Neascus* sp. (2), *N. rutili* (5), °*P. minimum* (2), *R. cascadilla* (1), °*Tetracotyle* sp. (1).

Paxton Creek 48(37): *A. lobatum* (33), Gyrodactyloidea (4), °Myxosporidia (1), *R. cascadilla* (4).

Hyas Lake 60(60): *A. lobatum* (1), °*Diplostomulum* sp. (59), Gyrodactyloidea (36), °Myxosporidia (19), °*Neascus* sp. (31), °*P. minimum* (60).

Pemberton Lake (1950) 42(42): °*Diplostomulum* sp. (28), Gyrodactyloidea (34), °*L. intestinalis* (2), °*Neascus* sp. (32), °*P. minimum* (42), °*Tetracotyle* sp. (2).

Pemberton Lake (1953) 52(51): *A. lobatum* (1), °*Diplostomulum* sp. (29), Gyrodactyloidea (9), °*L. intestinalis* (1), °*Neascus* sp. (35), °*P. minimum* (50), *R. cascadilla* (2).

Pinantun Lake (1946) 40(40): °*Diplostomulum* sp. (7), Gyrodactyloidea (19), °*L. intestinalis* (29), °*P. minimum* (40), *R. cascadilla* (12).

Pinantan Lake (1948) 35(35): °*Diplostomulum* sp. (11), °°*Eubothrium* sp. (1), Gyrodactyloidea (31), °*L. intestinalis* (20), °*Neascus* sp. (2), °*P. minimum* (35), *R. cascadilla* (8).

Pinantan Lake (1950) 40(40): °*Diplostomulum* sp. (10), Gyrodactyloidea (37), °*L. intestinalis* (23), *N. rutili* (13), °*P. minimum* (39), *R. cascadilla* (13).

Pinantan Lake (1953) 72(72): °*Diplostomulum* sp. (37), Gyrodactyloidea (66), °*L. intestinalis* (62), °Myxosporidia (1), °*Neascus* sp. (22), *N. rutili* (7), °*P. minimum* (72), *R. cascadilla* (69).

Paul Lake (1949) 31(28): *A. lobatum* (1), °*Diplostomulum* sp. (6), Gyrodactyloidea (20), °*L. intestinalis* (3), °Myxosporidia (2), °*P. minimum* (19), *R. cascadilla* (5).

Paul Lake (1950) 34(34): *A. lobatum* (1), °*Diplostomulum* sp. (25), Gyrodactyloidea (27), °*L. intestinalis* (8), °Myxosporidia (1), °*Neascus* sp. (1), °*P. minimum* (24), *R. cascadilla* (4).

Paul Lake (1953) 86(86): °*Diplostomulum* sp. (82), Gyrodactyloidea (72), °*L. intestinalis* (17), °*Neascus* sp. (28), °*P. minimum* (86), °°*Proteocephalus* sp. (1), *R. cascadilla* (80), °*Schistocephalus* sp. (1), °*Tetracotyle* sp. (7).

Skeena Drainage

Lakelse Lake 41(41): *A. lobatum* (1), °*Diplostomulum* sp. (35), Gyrodactyloidea (41), *H. bakeri* (1), °*L. intestinalis* (1), °*Neascus* sp. (6), *N rutili* (18), *Octomacrum* sp. (24), *P. bulbocolli* (7), °*P. minimum* (34), *R. cascadilla* (32), °*Spiroxys* sp. (7).

Peace Drainage

Swamp Creek 1(1): *R. cascadilla* (1).

The redside shiner from Swamp Creek was the first specimen of this fish recorded from the Peace River drainage and is so recorded by Carl and Clemens (1953).

During the two seasons a large number of redside shiners were examined. After the field work of 1953 a number of preserved collections were studied. The specimens from the Erie lake chain and those from the Pemberton–Pinantan–Paul Lake chain were collections of other years and gave us some information of changes in parasitism in various years.

Posthodiplostomum minimum was taken from the largest number of hosts, as 71 per cent of the redside shiners from 35 locations had this encysted fluke. *Diplostomulum* sp. was recovered from 39 per cent of the redside shiners from 25 locations, and the "black spot", *Neascus* sp., was found on 37 per cent of the fish examined. Gill flukes occurred on 59 per cent of the fish from 37 of the areas examined. *Ligula intestinalis* was taken in 13 per cent of the fish but the numbers were especially high in the shiners at Pinantan and Paul Lakes. At Pinantan Lake Kamloops Trout were taken that had recently eaten redside shiners infected with *Ligula*. Before the parasites could be digested they frequently penetrated the

stomach or intestine and several fish were found with these cestodes partly out into the body cavities of the trout. None had living *Ligula* in their body cavities.

Neoechinorhynchus rutili was recovered from 48 per cent of the shiners and from fish in 31 areas. Van Cleave and Lynch (1950) list as cyprinid hosts for *N. rutili*, *Mylocheilus caurinus* from King C. Washington and *Ptychocheilus oregonensis* from Cultus Lake, British Columbia. In most cases the forms obtained from the British Columbia shiners were adults but in certain lakes only young forms were found.

Octomacrum sp. was found on the gills of 8 per cent of the fish chiefly from the upper Columbia River drainage area. This appears to belong to an undescribed species and if so it will be described elsewhere.

The nematode, *Rhabdochona cascadilla*, was found in 37 per cent of the hosts from 34 locations. Fourteen other species of parasites were found in a small number of hosts in scattered locations.

A related species of minnow, *Richardsonius balteatus hydrophlox* was examined from 20 collecting stations in the Jackson Hole area (Bangham, 1951), and here 434 out of a total of 479 were infected with a total of 15 species of parasites. In order of frequency of occurrence the top ten parasites taken were: *P. minimum*, *R. cascadilla*, *Neascus* sp., *Contracaecum spiculigerum*, Gyrodactyloidea, *Clinostomum marginatum*, *Ergasilus caeruleus*, Myxosporidia, *Lebouria cooperi*, and *Allocreadium lobatum*.

23. **Brown Catfish** (Brown Bullhead). *Ameiurus nebulosus* (LeSueur)

Examined – 45 Infected – 40 Locations – 3

Fraser Drainage

Trout Lake (Vancouver) 5(5): *Corallobothrium fimbriatum* (5).
Mill Lake (Abbotsford) 35(30): *Alloglossidium corti* (1), *C. fimbriatum* (29), Gyrodactyloidea (6), *Phyllodistomum staffordi* (5).
Hatzic Lake 5(5): *C. fimbriatum* (5), *Neoechinorhynchus rutili* (1).

All of these fish were young individuals from the lower Fraser River area. *Corallobothrium fimbriatum* was the only parasite taken from brown bullheads in all stations. Only a single specimen of the fluke *Alloglossidium corti* was found.

In Wisconsin all of 49 brown bullheads from six locations were parasitized with a total of 16 different parasite species. The five species recovered from more than 20 per cent of the hosts were: Gyrodactyloidea, *C. fimbriatum*, *Alloglossidium geminus*, *Dichelyne robusta* and *Phyllodistomum staffordi*.

As has proven true for all introduced fishes examined during our British Columbia studies, the numbers of different parasites are lower than for the same species of fish in their native habitats.

Haderlie records the results of examination of 301 fish of this species from northern California. Of this number, 267 were parasitized. The following parasites were listed as common: *P. staffordi*, *Clinostomum marginatum*, *Diplostomulum corti*, *C. fimbriatum*, *Contracaecum spiculigerum*, *Illinobdella* sp., *Lernea carassii* with *A. corti* listed as an occasional parasite.

24. **Northern Black Catfish** (Black Bullhead). *Ameiurus melas melas* (Rafinesque)

Examined – 1 Infected – 1 Locations – 1

COLUMBIA DRAINAGE
Okanagan River (Oliver) 1(1): *Phyllodistomum staffordi* (1), *Rhabdochona* sp. (1).

Only one fish of this species was obtained on the survey. In Wisconsin, three black bullheads yielded a total of 8 parasite species and in Reelfoot Lake survey there were 13 different parasites taken from certain of the 11 hosts examined.

25. **Northern Pike.** *Esox lucius* Linnaeus

Examined – 2 Infected – 2 Locations – 1

LIARD DRAINAGE
Jackfish Creek (Mile 278, Alaska Highway) 2(2): *Proteocephalus pinguis* (2).

Two small specimens of northern pike yielded only the cestode *Proteocephalus pinguis*. This was the form secured most often by Bangham from 66 northern pike from the Manitoulin Lake survey where fish from five locations had 11 species of parasites. In Wisconsin 34 northern pike from seven locations carried a total of 12 parasite species with *P. pinguis* being recovered from 28 hosts.

26. **Three-spined Stickleback.** *Gasterosteus aculeatus* Linnaeus

Examined – 35 Infected – 31 Locations – 3

COASTAL STREAMS
Prudhomme Lake (Prince Rupert) 1(0).

SKEENA DRAINAGE
Lakelse Lake 32(31): *Bunoderina eucaliae* (7), Copepod (gills) (3), °*Diplostomulum* sp. (6), °*Eustrongylides* sp. (3), °Glochidia (10), Gyrodactyloidea (21), *Neoechinorhynchus rutili* (1), °*Posthodiplostomum minimum* (1), *Proteocephalus pugetensis* (19), °*Schistocephalus* sp. (9), °*Tetracotyle* sp. (7).

FRASER DRAINAGE
Silver Creek 2(0).

The three-spined sticklebacks from Lakelse Lake were the only hosts with parasites. This form has not been examined in any previous surveys by either of the authors. *Proteocephalus pugetensis* was first described from the Puget Sound area (Hoff and Hoff, 1929) and seems to be a typical western species. The other parasites are all of general distribution in North America.

27. **Brook Stickleback.** *Eucalia inconstans* (Kirtland)

Examined – 16 Infected – 7 Locations – 1

PEACE DRAINAGE
Charlie Lake (Fort St. John) 16(7): *Bunoderina eucaliae* (4), Gyrodactyloidea (1), °*Schistocephalus* sp. (3), °*Tetracotyle* sp. (3).

The only brook sticklebacks taken were from Charlie Lake and they showed parasite infection of a pattern similar to this species from other areas. In Wisconsin 20 of 28 from four locations yielded a total of 7 species of parasites with

Bunoderina eucaliae being found in 10 hosts. In the Manitoulin Island survey 34 brook sticklebacks were examined from a single location. Twenty-five carried *B. eucaliae*, 15 *Neoechinorhynchus rutili*, 8 gill flukes, 8 *Neascus* sp. and single hosts carried *Diplostomulum* sp. and *Posthodiplostomum minimum*.

28. **Ling** (Burbot). *Lota lota* Linnaeus

Examined – 30 Infected – 24 Locations – 8

Columbia Drainage

Hansen Lake (Cranbrook) 1(1): *Contracaecum brachyurum* (1), *Crepidostomum* sp. (1), °*Diplostomulum* sp. (1).

Vernon Creek (at Okanagan Lake) 1(1): °*Diplostomulum* sp. (1), *Eubothrium rugosum* (1).

Peace Drainage

Swamp Creek 11(6): *C. brachyurum* (6), °*Diplostomulum* sp. (1), °Myxosporidia (1).

Fraser Drainage

Creek from Nadsilnich Lake 9(8): °*Bothriocephalus* sp. (1), °*Diplostomulum* sp. (8), *Ergasilus caeruleus* (1), *E. rugosum* (2).

Dragon Lake 4(4): *Crepidostomum farionis* (1), °*Diplostomulum* sp. (4), °*Pomphorhynchus bulbocolli* (4), *P. bulbocolli* (1).

Chimney Lake 2(2): *C. farionis* (2), °*Diplostomulum* sp. (1), *Neoechinorhynchus rutili* (1), °*P. bulbocolli* (2), °*Posthodiplostomum minimum* (1).

Nicola River 1(1): *C. brachyurum* (1).

Shuswap Lake (Salmon Arm) 1(1): °*Diplostomulum* sp. (1), *E. rugosum* (1).

The parasites of this host were scattered, *Diplostomulum* sp. being taken from 57 per cent of the ling and from fish in all but one area. *Contracaecum brachyurum* was found in the intestinal tracts of 30 per cent of the hosts and in fish from three of the eight locations. Encysted *Pomphorhynchus bulbocolli* were found in all ling examined from two locations. The cestode, *Eubothrium rugosum*, frequently found in this host, was recovered from but four of the ling examined in British Columbia. *Haplonema hamulatum*, a nematode often taken from this fish in surveys in Eastern North America was not found. In the Manitoulin Lake survey 21 ling from two locations were parasitized with a total of 12 species. The four species most frequently recovered were: *E. rugosum*, *Echinorhynchus salmonis*, *Diplostomulum* sp., and *H. hamulatum*. In the examination of 15 ling from the Algonquin Park Lakes all were parasitized with a total of eight parasite species. Those recovered in from 5–15 hosts were: *E. rugosum*, *C. brachyurum*, *Leptorhynchoides thecatus*, *Ergasilus caeruleus*, *H. hamulatum* and *Hepaticola bakeri*.

29. **Yellow Perch.** *Perca flavescens* (Mitchill)

Examined – 16 Infected – 3 Locations – 1

Columbia Drainage

Smiths Pothole (Osoyoos) 16(3): °*Ligula intestinalis* (1), °*Neascus* sp. (3).

Yellow perch usually carry many species of parasites. In the Manitoulin Island survey 201 yellow perch from three locations had a total of 29 different

species of parasites and yellow perch from 29 locations in Wisconsin had 261 out of 269 parasitized with a total of 27 different parasites.

Haderlie found no parasites in 18 yellow perch examined in his California survey.

30. **Smallmouth Bass.** *Micropterus dolomieui* Lacépède

Examined – 10 Infected – 8 Locations – 1

Columbia Drainage

Christina Lake 10(8): °Cestode (not *P. ambloplitus*) (1), *Ergasilus caeruleus* (2), °°*Proteocephalus* sp. (1), *Rhabdochona* sp. (3).

The bass from Christina Lake, introduced in 1901 (Carl and Clemens, 1953), carried very light infections with four species of parasites. Haderlie records but three species from 31 small-mouth bass in California. *Proteocephalus microcephalus* was listed by him as abundant, *Lernea carassii* as occasional and *Posthodiplostomum minimum* as rare.

The relative absence of parasites in the smallmouth introduced on the west coast is to be seen in comparing the above data with records from eastern North America. Thus Bangham reports that 44 smallmouth bass from eight locations in Wisconsin yielded 24 different parasite species. In the 1951 survey at Manitoulin all but one host out of 221 from 12 collecting sites in Lake Huron and lakes on the island yielded a total of 30 parasite species.

31. **Largemouth Bass.** *Micropterus salmoides* Lacépède

Examined – 48 Infected – 47 Locations – 3

Columbia Drainage

Smiths Pothole (Osoyoos) 16(16): Gyrodactyloidea (16), °*Proteocephalus ambloplitis* (4).

Shannon Lake (Westbank) 10(10): Gyrodactyloidea (10).

Duck Lake outlet (at Kootenay Lake) 22(21): °*Diplostomulum* sp. (7), Gyrodactyloidea (8), °*Neascus* sp. (1), °*Proteocephalus ambloplitis* (16).

These fish from three locations showed light infections with but few of their natural parasites. Gill flukes were found on hosts from each area and the bass cestode *Proteocephalus ambloplitis* was recovered as larval cysts. No adults were found. Haderlie examined 145 largemouth bass and parasites were obtained from 98. The list of different forms is short when compared with this host in its native habitats. He lists a total of six different parasite species.

In the Wisconsin survey 26 species were recorded for largemouth bass from 17 locations. There were 98 of 102 individuals that were parasitized. In the Reelfoot Lake survey a total of 20 species of parasites were found in 69 largemouth bass from that lake. In Florida all of 86 bass were parasitized with a total of 19 species.

32. **Pumpkinseed** (Sunfish). *Lepomis gibbosus* (Linnaeus)

Examined – 22 Infected – 16 Locations – 2

Columbia Drainage

Smiths Pothole (Osoyoos) 15(11): Gyrodactyloidea (5), °*Neascus* sp. (2), °*Posthodiplostomum minimum* (8), °*Spiroxys* sp. (1).

Okanagan River (Oliver) 7(5): Gyrodactyloidea (4), °*Neascus* sp. (1), °*P. minimum* (4).

All the parasites except the gill flukes were larval encysted forms. Pumpkinseed in eastern North America usually have a variety of parasites with a majority of encysted forms, but they also carry several species of adult nematodes, flukes, and frequently acanthocephalans and cestodes.

In Algonquin Park 35 pumpkinseeds from seven lakes had a total of 16 parasite species. In Wisconsin pumpkinseeds from 15 locations in northern areas yielded from 76 hosts, 26 different parasitic forms.

33. **Black Crappie.** *Pomoxis nigro-maculatus* (LeSueur)

Examined – 40 Infected – 25 Locations – 2

Fraser Drainage

Trout Lake (Vancouver) 27(23): Gyrodactyloidea (23).
Hatzic Lake 13(2): Gyrodactyloidea (2).

Gill flukes were the only forms recovered from 25 of 40 black crappies examined during this survey. Black crappies frequently have fewer parasites than other Centrarchidae, but in Wisconsin from 10 locations 63 of 67 black crappies carried a total of 10 species of parasites. In Reelfoot Lake 15 of 19 hosts had a total of 11 parasite species. All had very light infections. In Manitoulin Island two black crappies yielded six parasite species.

Haderlie examined 69 California black crappies with 48 infected with at least one species of parasite. The most abundant form was *Contracaecum spiculigerum* with *Paramphistomum stunkardi* and *Lernea carassii* recorded as occasional. A few immature *Proteocephalus* sp. were also taken.

34. **Prickly Sculpin.** *Cottus asper* Richardson

Examined – 344 Infected – 275 Locations – 25

Columbia Drainage

Christina Lake 4(2): *Crepidostomum isostomum* (1), Gyrodactyloidea (1), *Rhabdochona cotti* (1).
Borgeson Lake (Princeton 30(30): °*Diplostomulum* sp. (30), *Ergasilus* sp. (1), °Myxosporidia (1), *Neoechinorhynchus rutili* (1), *Pomphorhynchus bulbocolli* (15), °*Tetracotyle* sp. (20).
Allison Creek 3(3): *Cyathocephalus truncatus* (1), Gyrodactyloidea (2), *R. cotti* (2).
Okanagan River (Oliver) 10(5): °Myxosporidia (3), °°*Proteocephalus* sp. (1), *Salmincola* sp. (3).
Twin Lake 3(0).
Deep Creek (Peachland) 3(3): °*Diplostomulum* sp. (2), Gyrodactyloidea (2).
Vernon Creek (at Wood Lake) 5(5): Gyrodactyloidea (4), °°*Proteocephalus* sp. (2).
Vernon Creek (at Okanagan Lake) 14(14): *Bothriocephalus* sp. (2), °*Diplostomulum* sp. (14), Gyrodactyloidea (5), °Myxosporidia (3), *N. rutili* (2), °*Posthodiplostomum minimum* (1), °°*Proteocephalus* sp. (9), *R. cotti* (1), °*Tetracotyle* sp. (1).
Otter Creek (Vernon) 4(3): °°*Proteocephalus* sp. (3).

Coastal Streams

Port John (near Bella Bella) 27(6): °*Eustrongylides* sp. (3), *Hepaticola bakeri* (3).
Prudhomme Lake (Prince Rupert) 1(1): °*Eustrongylides* sp. (1).

Skeena Drainage

Lakelse Lake 25(24): °*Diplostomulum* sp. (22), °*Eustrongylides* sp. (10), °Glochidia (1), *H. bakeri* (3), *Metabronema salvelini* (1), °Myxosporidia (2), *N. rutili* (1), °*Schistocephalus* sp. (3), °*Tetracotyle* sp. (7).

Kathlyn Lake (Smithers) 12(12): °*Diplostomulum* sp. (10), °*Eustrongylides* sp. (1), °*Schistocephalus* sp. (1), °*Tetracotyle* sp. (10).

PEACE DRAINAGE

Swamp Creek 2(0).

FRASER DRAINAGE

Middle River (Takla Lake) 27(22): *Bothriocephalus* sp. (1), *C. isostomum* (6), °*Diplostomulum* sp. (14), °°*Eubothrium* sp. (1), °*Eustrongylides* sp. (2), °Glochidia (3), *H. bakeri* (5), °Myxosporidia (1), *N. rutili* (3), °°*Proteocephalus* sp. (3), *R. cotti* (1), °*Schistocephalus* sp. (1), °*Tetracotyle* sp. (2).

Cluculz Lake 1(1): °*Diplostomulum* sp. (1).

Deep Creek (Cluculz Lake) 18(18): °*Diplostomulum* sp. (18), *Ergasilus* sp. (2), °*Eustrongylides* sp. (1), °Glochidia (1), *H. bakeri* (3), °Myxosporidia (1), *P. bulbocolli* (1), °*Tetracotyle* sp. (4).

Joseph Creek (at Nadsilnich Lake) 14(14): °*Diplostomulum* sp. (14), °Myxosporidia (1), *R. cotti* (1), °*Schistocephalus* sp. (1), °*Tetracotyle* sp. (14).

Campbell Creek (Kamloops) 32(15): °*Diplostomulum* sp. (15), °*Eustrongylides* sp. (6), °Myxosporidia (1).

Davis Creek 7(1): °*Schistocephalus* sp. (1).

Shumway Lake 27(23): °*Diplostomulum* sp. (22), °Myxosporidia (1), °*Tetracotyle* sp. (1).

Trapp Lake 15(14): °*Diplostomulum* sp. (14), °°*Proteocephalus* sp. (3), °*Tetracotyle* sp. (3).

Pringle Creek 39(39): °*Diplostomulum* sp. (39), °Myxosporidia (2), °*Schistocephalus* sp. (2), °*Tetracotyle* sp. (14).

Salmon River 1(1): °*Tetracotyle* sp. (1).

Hatzic Lake 20(19): °*Eustrongylides* sp. (11), *H. bakeri* (3), °*Schistocephalus* sp. (4), °*Tetracotyle* sp. (10).

Over half of the parasites reported were recovered from a few hosts in but one or two of the 25 locations. Eye flukes were recovered from 63 per cent of the hosts in 13 areas. *Eustrongylides* sp., an encysted red nematode, was found in 10 per cent of these sculpins from eight areas, but was not taken in the Columbia drainage. *Tetracotyle* sp. cysts were found in 25 per cent of individuals from 12 locations. *Rhabdochona cotti* was described for *Cottus cognatus* from the Griffith Springs State Fish Hatchery near Spokane, Washington, by Gustafson (1949). Dr. Gustafson has confirmed our identification of this species.

The three *Cottus asper* examined by Haderlie were entirely free of parasites.

35. **Torrent Sculpin.** *Cottus rhotheus* (Rosa Smith)

Examined – 38 Infected – 38 Locations – 1

COLUMBIA DRAINAGE

Dry Lake (Princeton) 38(38): °*Diplostomulum* sp. (38), Gyrodactyloidea (7), *Neoechinorhynchus rutili* (2), *Pomphorhynchus bulbocolli* (18), °°*Proteocephalus* sp. (10), °*Tetracotyle* sp. (32).

36. **Mottled Sculpin.** *Cottus cognatus* Richardson

Examined – 49 Infected – 29 Locations – 3

COLUMBIA DRAINAGE

Christina Lake 4(3): Gyrodactyloidea (2), *Rhabdochona cotti* (2).

Erie Creek 17(1): °Fluke metacercaria (1).

LIARD DRAINAGE

Jackfish Creek (Alaska Highway) 28(25): *Haplonema* sp. (4), *R. cotti* (22).

CHECK LIST OF PARASITES WITH HOST REFERENCES

Numbers following the names of the parasites refer to the numbers given to host species in the host list.

TREMATODA

Gyrodactyloidea (2, 3, 5, 8, 11, 13, 14, 16, 17, 18, 19, 20, 21, 22, 23, 26, 27, 31, 32, 33, 34, 35, 36)
Dactylogyrus extensus Mueller and Van Cleave, 1932 (16)
Discocotyle salmonis Schaffer, 1916 (2, 11)
Octomacrum sp. (19, 22)
Octomacrum lanceatum Mueller, 1934 (13, 14, 17)
Bucephalopsis ozarkii (Nagaty, 1937) (11)
Phyllodistomum staffordi Pearse, 1924 (23, 24)
Plagiocirrus sp. (13)
Allocreadium lobatum Wallin, 1909 (2, 9, 13, 17, 19, 21, 22)
Crepidostomum farionis (O. F. Müller, 1784) (2, 3, 5, 6, 7, 8, 9, 10, 11, 28)
Crepidostomum isostomum Hopkins, 1931 (34)
Crepidostomum sp. (4, 28)
Triganodistomum attenuatum Mueller and Van Cleave, 1932 (13, 14)
Alloglossidium corti (Lamont, 1921) (23)
Brachyphallus crenatus (Rudolphi, 1802) (11)
Lecithaster salmonis Yamaguti, 1934 (6, 11)
Bunoderina eucaliae Miller, 1936 (26, 27)
Clinostomum marginatum (Rudolphi, 1819) (17, 22)
Diplostomulum sp. (2, 3, 5, 8, 9, 10, 11, 13, 14, 15, 17, 19, 21, 22, 26, 28, 31, 34, 35)
Posthodiplostomum minimum (MacCallum, 1921) (13, 14, 17, 18, 19, 20, 21, 22, 26, 28, 32, 34)
Tetracotyle sp. (2, 6, 11, 13, 14, 17, 19, 21, 22, 26, 27, 34, 35)
Neascus sp. (8, 10, 11, 13, 14, 17, 18, 19, 20, 21, 22, 29, 31, 32)

CESTODA

Corallobothrium fimbriatum Essex, 1927 (23)
Proteocephalus ambloplitis (Leidy, 1887) (31)
Proteocephalus exiguus LaRue, 1919 (2, 7)
Proteocephalus laruei Faust, 1920 (7)
Proteocephalus pinguis LaRue, 1911 (25)
Proteocephalus pugetensis Hoff and Hoff, 1929 (26)
Proteocephalus ptychocheilus Faust, 1920 (17, 21)
Proteocephalus sp. (3, 5, 6, 7, 19, 22, 30, 34, 35)
Proteocephalus salmonidicola Alexander, 1951 (8, 9, 11)
Phyllobothrium sp. (1, 6, 11)
Hymenolepis sp. (19)
Caryophyllaeus terebrans (Linton, 1893) (13, 14, 16, 17)
Glaridacris catostomi Cooper, 1920 (13, 14, 15)
Cyathocephalus truncatus Kraemer, 1892 (34)
Ligula intestinalis (Linnaeus, 1758) (2, 10, 13, 14, 17, 19, 21, 22, 29)
Diphyllobothrium sp. (2, 5, 6, 7, 8, 9, 11, 12)
Bothriocephalus sp. (28, 34)
Schistocephalus sp. (2, 7, 9, 13, 22, 26, 27, 34)
Eubothrium salvelini (Schrank, 1790) (8, 9, 11, 12, 17, 21)
Eubothrium rugosum (Batsch, 1786) (28)
Eubothrium sp. (2, 6, 7, 13, 19, 22, 34)

NEMATODA

Hepaticola bakeri Mueller and Van Cleave, 1932 (2, 5, 8, 9, 10, 11, 13, 14, 17, 19, 21, 22, 34)
Contracaecum brachyurum (Ward and Magath, 1917) (28)
Contracaecum spiculigerum (Rudolphi, 1809) (6, 21)
Contracaecum sp. (8, 11)
Contracaecum sp. (cyst) (11)
Metabronema salvelini (Fujita, 1920) (2, 3, 5, 6, 7, 8, 9, 10, 11, 20, 34)
Metabronema sp. (4)
Cystidicola stigmatura (Leidy, 1886) (2, 3, 9)
Rhabdochona cascadilla Wigdor, 1918 (6, 7, 8, 9, 13, 14, 16, 17, 18, 19, 20, 21, 22)
Rhabdochona cotti Gustafson, 1949 (34, 36)
Rhabdochona sp. (2, 5, 10, 24, 30)
Spiroxys sp. (cyst) (14, 21, 22, 32)
Bulbodacnitis globosa (Zeder, 1800) (2, 3, 8, 9, 10, 11)
Bulbodacnitis sp. (17, 20, 22)
Bulbodacnitis sp. (cyst) (20)
Haplonema sp. (immature) (36)
Philonema oncorhynchi Kuitunen-Ekbaum, 1933 (5, 6, 7, 8, 9, 11)
Philonema sp. (2, 3, 18)
Eustrongylides sp. (1, 2, 3, 8, 11, 12, 14, 15, 17, 26, 34)

ACANTHOCEPHALA

Neoechinorhynchus rutili (O. F. Müller, 1780) (2, 5, 6, 7, 8, 9, 10, 11, 13, 14, 17, 19, 21, 22, 23, 26, 28, 34, 35)
Neoechinorhynchus cristatus Lynch, 1936 (13, 14, 17)
Neoechinorhynchus venustus Lynch, 1936 (14, 17)
Neoechinorhynchus crassus Van Cleave, 1919 (14)
Pomphorhynchus bulbocolli Linkins, 1919 (2, 5, 8, 9, 13, 14, 15, 17, 21, 22, 28, 34, 35)

COPEPODA

Ergasilus caeruleus Wilson, 1911 (7, 9, 13, 14, 17, 18, 19, 21, 22, 28, 30)
Ergasilus sp. (2, 34)
Achtheres coregoni (S. I. Smith, 1874) (2, 3)
Salmincola edwardsi (Olsson, 1869) (8, 9, 11)
Salmincola sp. (2, 6, 7, 12, 26, 34)

MOLLUSCA

Glochidia (9, 17, 19, 21, 22, 26, 34)

PROTOZOA

Myxosporidia (2, 6, 8, 11, 13, 14, 15, 17, 19, 20, 21, 22, 28, 34)
Trichodina sp. (16)

ANNELIDA

Actinobdella trianulata Moore, 1905 (13, 14)
Illinobdella sp. (9, 21)

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The Amphipod Crustacea of Ungava Bay, Canadian Eastern Arctic[1,2]

"CALANUS" SERIES NO. 6

BY M. J. DUNBAR
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ABSTRACT

One hundred and fourteen species of amphipods are recorded from Ungava Bay, most of them for the first time from that area; 21 are new for North America, 5 new to science. Many of them show variations from the types, the types having been described from European or Greenland material. Such variations are to be expected in the Ungava Bay material since it represents a large extension in the known distribution of most of the species, and especially in groups such as the Gammarid and Caprellid amphipods which have no pelagic larvae.

In two cases (*Westwoodilla megalops* and *Haploops setosa*) pairs of amphipod forms known from Europe as separate species are represented in Ungava Bay by forms which cannot without qualification be referred to either European form, showing characteristics of both, and the two species have therefore been brought into synonymy in each case, since the situation does not warrant the establishment of new species for the Ungava Bay specimens. Since in both cases the European forms were very close together in the first place, each of the two species now exists as three geographic variants; subspecific names have not been given to the variants. Evidence is produced in favour of bringing three species of *Ischyrocerus* (*I. latipes, I. assimilis* and *I. pachtusovi*) together into a similar species complex.

The distribution of the Ungava Bay amphipods is analysed. They can be divided into (1) an Atlantic group, possibly endemic to the Atlantic, (2) a group whose distribution lies within the subarctic marine zone as here defined, (3) a large group which does not appear to extend south of the subarctic on the western side of the Atlantic but which is widely distributed in the boreal on the eastern side, in the North Sea area, (4) a small number of arctic forms which become less abundant in the subarctic, and (5) species probably of Pacific origin which are not known east of Greenland nor west of the Kara Sea.

INTRODUCTION

THE *Calanus* expeditions of 1947–50, which provided the material described here, operated mainly in the waters of Ungava Bay. The station list for these four years has already been published (Dunbar and Grainger, 1952), together with the necessary maps. All station numbers and place names in this present paper, unless specifically qualified, will be found in the station list.

The collection includes planktonic, littoral and benthonic forms, taken with non-closing plankton nets (one-metre stramin, and silk nets numbers 0, 5, 6 and 18) towed for the most part horizontally, dredges and to a much lesser extent beam-trawls and otter-trawls; and shore collecting by hand. Amphipods from stomachs of Atlantic cod and from seals are also included here.

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Apart from the new species described, there are many examples of variation from the types and from standard descriptions. Since the latter are based very often on specimens from northwest Europe, such variations are to be expected in material from an area hitherto very little investigated, especially in the amphipods, whose systematics are complicated by post-maturation moults. Whenever possible, the variants have been compared directly with specimens from Europe, Iceland and Greenland contained in the very large collections of the Zoological Museum, Copenhagen University. The terms "Copenhagen material" and "Copenhagen specimens" in the present paper refer to that collection.

There is still a lack of unanimity in naming the limbs of the Amphipoda. The matter is discussed by Spooner (1947), with whose conclusions and practice I am in agreement. Gnathopods 1 and 2, being the first limbs of the peraeon, are peraeopods, and should therefore be numbered in series with the other five peraeopods, as is done by Stephensen, but not by Stebbing (1906). Sars (1895) numbers the appendages of the mesosome (peraeon) "pes 1 to pes 7", but in the text he divides them into "gnathopods 1 and 2" and "peraeopods 1 to 5", thus repeating the confusion found in Stebbing. In this present paper the limbs of the mesosome are numbered from 1 to 7, and they are called peraeopods, or abbreviated to "per."

All measurements given are made from the front of the head, or tip of the rostrum, to the tip of the last uropods.

The terms "arctic" and "subarctic" are here used according to the criterion and practice already published (Dunbar, 1951, 1953); "arctic" referring to marine areas of shelf depths in which the water is of polar (Arctic Sea) origin (ignoring land drainage) unmixed with Atlantic or Pacific water; "subarctic" referring to areas in which the water of shelf depths consists of both polar and non-polar (Atlantic or Pacific) water. South of the subarctic is the large boreal marine region, extending to the subtropics. For the delimitation of these arctic and subarctic regions, see the papers quoted.

Sub-order *Gammaridea*

Family LYSIANASSIDAE

Opisa eschrichti (Krøyer)

One mature female, dredged in 18–20 metres at station 216, Diana Bay, from rocky bottom with mud, July 24, 1950.

The specimen differs from the original description, from the synopsis in Stebbing (1906) and from the Sars figure (Sars, 1895) in that the second joint of the mandibular palp is not "strongly setiferous"; the third joint, on the other hand, is richly supplied with setae. Specimens examined from Godthaab, west Greenland, in the collection of the Zoological Museum of Copenhagen, have a few setae on the second joint, but nothing like the setation shown in Sars, and a slight, not strong, setation of the third joint. In the Diana Bay specimen the

second joint is almost naked and the third joint shows as rich setation as Sars and Stebbing describe for the second joint.

The species appears to be boreal and subarctic in distribution, being known from west Greenland (Godthaab and Holsteinsborg, 1892), east Iceland, the Faeroes, the North Sea and the Norwegian coast, Kola Bay and the White Sea (Stephensen, 1923, 1935; Derjugin, 1915, 1928). It is also recorded from Monterey Bay on the Pacific coast (Shoemaker, 1930a), the Korea Sea and the Sea of Japan (Derjavin, 1930). Shoemaker (1930a) recorded it for the first time from eastern North America (Gulf of St. Lawrence and coast of Nova Scotia). Stephensen (1935) calls it "probably circumpolar", but it has not been found yet either in east Greenland or in the arctic part of the Siberian shelf, and its present known distribution does not show it in any truly arctic region.

Onisimus edwardsi (Krøyer)

Taken both planktonically and in the dredge; in plankton nets, at stations 9, 51, 101 and 123, hauling at depths from 5 to 13 metres in shallow water, one specimen in each haul. Twenty-five specimens were dredged at station 125A (Payne Bay) on August 23, 1949, in 14 metres, and 42 specimens were taken on the skull of a beluga (*Delphinapterus leucas*) lowered to the bottom overnight in 20 metres at station 212, for cleaning. Many hundreds were taken in a similar manner on a seal skull at station 124. All specimens taken were immature.

Onisimus edwardsi is probably circumpolar, although there are still gaps in its known distribution, notably on the Siberian shelf and in the Canadian central arctic. It is found in both arctic and subarctic regions, and extends also into the boreal, in southwest Norway and the Kattegat. In eastern Canada, it has been taken in northwest Hudson Bay, the Labrador coast and the Gulf of St. Lawrence (Shoemaker, 1930a), southeast of Cape Sable and on the Grand Bank (Shoemaker, 1930b).

Onisimus plautus (Krøyer). (Fig. 1)

Forty-five specimens were taken altogether, at stations 20, 45, 102 and 216, all in the benthos at depths varying from 10 to 70 metres. Mature females with eggs were taken at station 102, June 6, 1949 (one specimen), and at station 216, July 7, 1950 (one specimen). Four specimens were taken from stomachs of the Atlantic cod (*Gadus callarias*) at Port Burwell.

The Ungava Bay specimens differ from the type and from other specimens from west Greenland in the Copenhagen University collection in the shape of joint 6, pes 1, which is somewhat longer in proportion to width in the present material, and with a slightly more sloping palm. In this character the specimens are in agreement with the figure published by Shoemaker (1930b) from specimens from Newfoundland and Nova Scotia, and it is probable that we have here an eastern North American variant of the species, which was first described from Greenland. The two forms of the joint in question are shown in Figure 1.

Onisimus plautus is probably circumpolar, arctic and subarctic. In arctic water it is known from northeast Greenland, from east of the 90th meridian on the Siberian shelf, from western Baffin Bay, Prince Regent Inlet, Foxe Basin and Dolphin and Union Strait (Gurjanova, 1932; Shoemaker, 1920). It is widely

distributed in the subarctic, including Bering Strait, and like the preceding species it extends south of the subarctic into the Skagerak, possibly as an arctic relict. Shoemaker (1930a, 1930b) has recorded it from the Gulf of St. Lawrence, Newfoundland and Nova Scotia.

FIGURE 1. *Onisimus plautus*, per. 1, from Greenland (left) and Ungava Bay (right).

Onisimus affinis H. J. Hansen

Syn.: *Onisimus botkini* Birula.

Six specimens were taken at station 229 (Adlorilik Inlet), on August 28, 1950, collected by hand at low tide on a sandy shore with rocks and seaweed, and with small freshwater streams. Numbers of *Pseudalibrotus littoralis* were collected at the same station. The specimens are all immature, the largest 14 mm. long.

Stephensen (1923) suggested tentatively that the *Onisimus affinis* of Hansen, of which the type is in Copenhagen, is a young *botkini*. Working later on the Fifth Thule Expedition material (Stephensen, 1937) he put the two species unequivocally together. Gurjanova (1932), however, keeps them apart, separating them on the shape of the last epimeral plate (pleon 3), acutely upturned in *affinis* and rounded in *botkini*. After examining the material in the Copenhagen Museum, including the Fifth Thule specimens from King William Island, and the present specimens from Ungava Bay, I agree with Stephensen that the two

should be considered synonymous. The shape of pleon 3 shows variation from fairly sharp to rounded, and the extent to which it is produced may be great or small. In the present material it is produced to a rounded point, as in the type specimen of *affinis*, and as figured by Shoemaker (1920) for *botkini*.

This species is known from the Kara Sea, the Siberian coast to the Bering Strait, northeast Greenland and Jan Mayen (Stephensen, 1923; Gurjanova, 1932); from Demarcation Point and Collinson Point, Alaska (Shoemaker, 1920), King William Island (Stephensen, 1937) and now from Ungava Bay. Gurjanova (1935b) states that, together with several other species of *Onisimus*, it is found in brackish water regions along the coast, especially at the mouths of rivers and streams. The Ungava Bay station agrees with this, but it has been found elsewhere in greater depths, down to 40 metres, occasionally deeper still (Stephensen, 1923). It is circumpolar arctic, also invading the subarctic.

Pseudalibrotus littoralis (Krøyer)

A very abundant species, especially in shallow water and in the intertidal zone. In Ungava Bay it was taken, often in large numbers, at the following stations: In plankton nets, at stations 1, 6, 18, 31, 40, 43, 44 and 51; and in the littoral zone at stations 107A, 107B, 215, 217 and 229. It was never taken far from the shore, and at all littoral stations at which it was collected there was a strong freshwater influence; often the specimens were collected in freshwater streams. It appears to be the rule that in the subarctic, which is the southern limit of the distribution of *Pseudalibrotus littoralis*, it is found in brackish areas only.

The species is arctic and subarctic in distribution, but it is not strictly speaking circumpolar. However, the form which replaces it between Novaya Zemlya and eastern Siberia, i.e. *P. birulai*, which has been given full specific rank by Gurjanova (1929), is very close to *littoralis*. The southern limit of *littoralis* in Canada is not known, but is presumably on the Labrador coast. It is not known from the Gulf of St. Lawrence. It was taken in northern Alaska and the Canadian central arctic by the Canadian Arctic Expedition (Shoemaker, 1920).

Specimens over 20 mm. in length were taken in Ungava Bay, but no specimen was mature. Specimens taken on August 29, 1947, had the lengthening antennae of the male, and there may be a breeding period late in the season.

Pseudalibrotus glacialis G. O. Sars

Fifty-six specimens of this species were taken, all in the plankton, at stations 1, 6, 7, 9, 13, 18, 41, 57, 203 and 221. Most were captured in 1947; not a single specimen was taken in 1949, although the total amount of plankton collected during that season was almost as large as in 1947. One specimen was taken from a cod stomach at Port Burwell.

This species is always more abundant than *P. nanseni* in Ungava Bay. Both are pelagic; *P. glacialis* is the more southerly of the two. Since their first description by Sars (1900), the diagnostic characters have been slightly revised, by Stephensen (1923) and Dunbar (1942). The presence of apical spines on the telson in the male is not invariable, and the female, which was described by Sars as without the spines, very often has them. The largest specimens taken had the third epimeral plate somewhat more acute than figured by Sars (1900) and drawn out slightly into a fine point. All specimens were immature, in the months of July and August. Mature females have been taken in southeast Baffin Island in September (Dunbar, 1942), and it is clear that there is a breeding period late

in the summer. The species has recently been recorded from the Strait of Belle Isle (Bousfield, 1951).

Pseudalibrotus nanseni G. O. Sars

Five specimens were taken in Ungava Bay, all immature. Two were caught in plankton nets, at stations 9 and 18; three in cod stomachs at Port Burwell.

This is an arctic pelagic species, and is possibly a useful indicator of arctic water when found in the surface layers. The distribution, which is circumpolar, is given in a map published by Gurjanova (1932), to which should now be added the present record from Ungava Bay and previous records from Hudson Strait and Frobisher Bay (Dunbar, 1942).

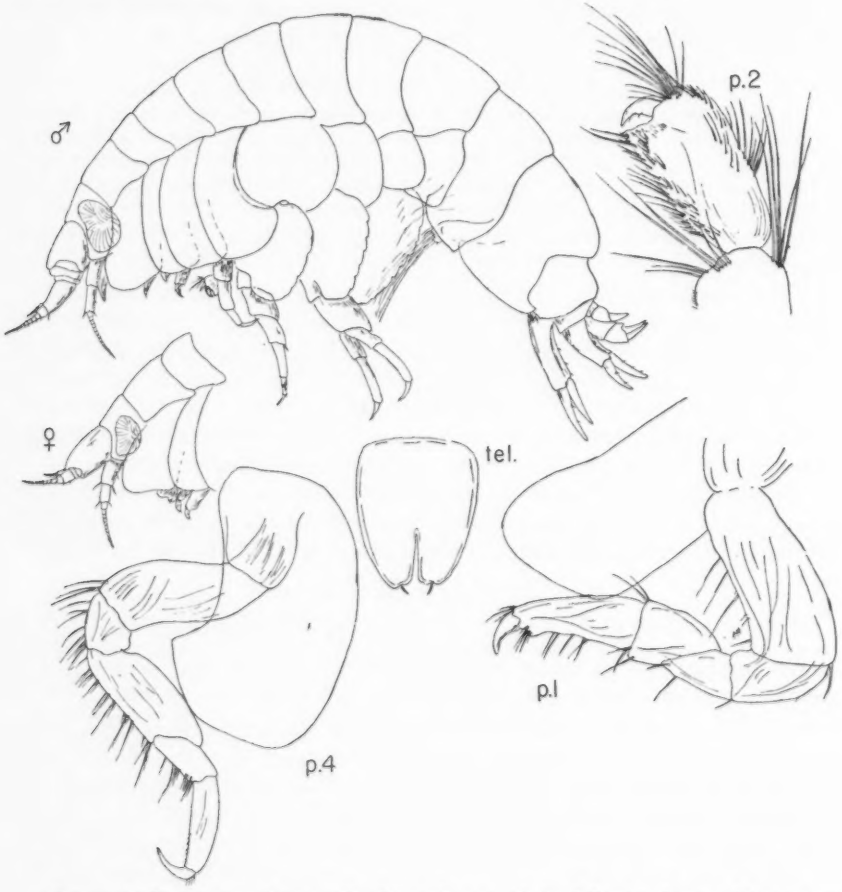

FIGURE 2. *Paronesimus barentsi*. In this and many of the following figures abbreviations are used as follows: ant., antennae: u.l., upper lip: l.l., lower lip: md., mandible: mx.1, mx.2, maxilla 1 and 2: mxp., maxillipeds: p.1, 2, 3, etc., peraeopod 1, 2, 3, etc.: sp., side-plate: pl.3, pleon 3: ur. uropod: tel., telson.

Paronesimus barentsi Stebbing. (Fig. 2 and 3)

This rare species was taken three times in the dredge and once in the shrimp beam-trawl, as follows: station 20 (60 metres, July 18, 1947, 4 specimens); station 45 (about 12 metres, August 23, 1947, 1 specimen); station 102 (90–120 metres, June 30, 1949, 5 specimens). Both the beam-trawl and the dredge were used at the latter station. In all four hauls, *Onisimus plautus* was also taken. The specimen taken on August 23, 1947, is a female, almost mature.

This species has been recorded only twice in the past, both records being from the vicinity of Novaya Zemlya. The type specimen was described by Stebbing (1894) from west of Novaya Zemlya, and Gurjanova (1936a) has recorded it from the Kara Sea. Its presence in Ungava Bay is therefore of great interest. Stebbing's original description and figures are very full, and the variations which the present specimens show from the original are detailed below and are illustrated in the accompanying figures. They might, in the hands of another systematist, be considered sufficient to justify the erection of a new subspecies.

Stebbing (1894) describes the genus, erected by him, as follows:

The genus stands near to *Onisimus* Boeck and *Chironesimus* Sars. It is distinguished from *Onisimus* by having the palp much longer than the trunk in the mandibles, by having the

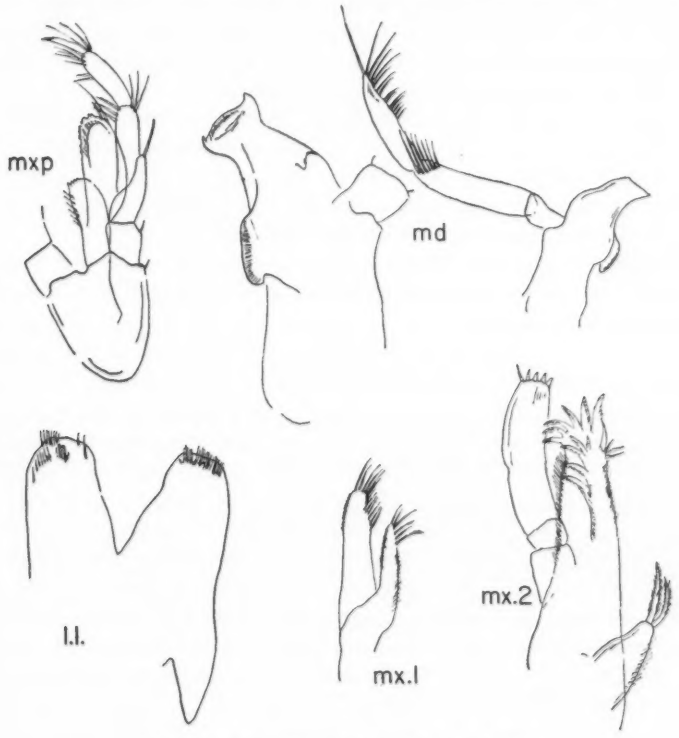

FIGURE 3. *Paronesimus barentsi*, mouthparts.

palp of the first maxillae more elongate and with fewer spines on the apex, by the truncate palm of the second gnathopods, and by the telson which is much longer than broad and incised for more than a third but less than half of the length. From *Chironesimus*, which it strongly resembles in general appearance, it is distinguished by fewer spines on the palp of the first maxillae, by narrower second maxillae, by a different shape and armature of the outer plate of the maxillipeds, by the less deeply cleft telson and the smaller uropods.

In all these characters the Ungava Bay specimens are in agreement, and they agree also in detail with Stebbing's description and figures of *barentsi*, except for the following three points: In the female, the first joint of the flagellum of the first antenna is not as long as the next three joints; in the male, this joint is longer than the next three joints, as described by Stebbing. The apices of the lower lip are hairy, although not richly so. Stebbing describes them as "apparently smooth", suggesting that his specimen was slightly damaged in this respect (it was apparently damaged also in the eyes and the first antennae). In per. 2 the finger, or seventh joint, is not so strongly curved as in Stebbing's specimen.

Quoting again from Stebbing: "The shape of the eyes is believed to be the same as in the species just mentioned" (*Chironesimus debruynii* (Hoek)). The eyes in the present material are fairly large, broader than in *Chironesimus*. The general appearance, as Stebbing records, is similar to *Chironesimus*, except for the shape of the eye, the much shorter head, the blunter and less produced lateral angles of the head, and the shape of side-plate 4, which is characteristically narrow, with the posterior expansion short and blunt.

The presence of this species in Ungava Bay agrees with the distribution of certain other species described below (see summary). It is probably a species of Pacific origin which has spread both east and west from the Bering Sea along the Siberian and North American coasts, and it is to be expected that it will be taken in due course in eastern Siberia and Alaska.

Stebbing gives no size for his type specimen. The Ungava Bay specimen drawn here (Fig. 2) is 11.25 mm. in length, and the largest specimen taken, a female, measures 14.75 mm.

Orchomene macroserrata Shoemaker. (Fig. 4)

Five specimens, taken at stations 3, 20, 28 and 203, in the dredge. One badly damaged specimen, almost entirely eaten away on one side, was taken in a plankton net at station 18. All the specimens are immature, one female with incompletely developed brood lamellae.

Shoemaker (1930b) established this species on material from the vicinity of Grand Manan, Bay of Fundy. It is very close to *O. tschernyschevi* Brüggen, 1909, recorded from Jugor Strait, between the island of Waigatsch and the mainland of Siberia. It is in fact so close to the Siberian species as to be another example of the type of distribution mentioned above, for *Paronesimus barentsi*. *O. macroserrata* differs from *tschernyschevi* only in the shorter lobe on joint 5, per. 1 (gnathopod 1), and the larger and fewer serrations on the postero-lateral margin of pleon 3. These characters in both species are illustrated in Figure 4. *O. macroserrata* is known so far only from the Bay of Fundy and from Ungava

Bay; *O. tschernyschevi* has not been recorded since the original record from Jugor Strait.

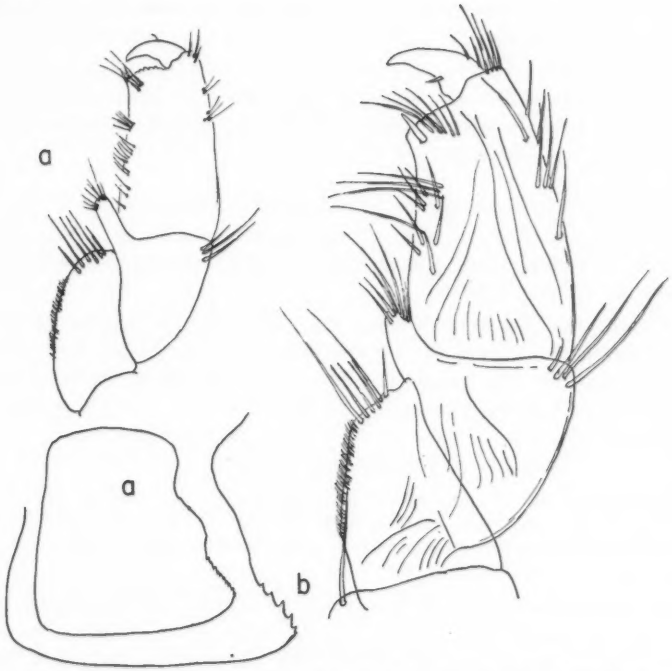

FIGURE 4. a: *Orchomene tschernyschevi*, per. 1 and telson, after Brüggen, 1909.
b: *Orchomene macroserrata*, per. 1 and telson.

Aristias tumidus (Krøyer)

Ten females, apparently not quite mature, and three immature specimens, were dredged on August 13, 1950, at station 226 (Button Islands) in 90–100 metres.

This species is circumpolar arctic and subarctic in distribution, known from the Newfoundland banks, west Greenland, east Greenland, Jan Mayen, west and north Svalbard, north Norway, the Barents and Kara Seas, Kola Bay, always in fairly shallow water. For details of localities see Stephensen (1935).

Anonyx nugax (Phipps)

This very common species was taken in the dredge at the following stations: 11, 20–21, 27, 102, 201C, 216, 225 and 231, in depths between 5 and 130 metres. Specimens were also taken from seal and beluga skulls in process of cleaning at stations 124 and 125A, and 64 individuals, some fully mature, were found in the stomach of an eider duck female (*Somateria mollissima*) at Port Burwell, July 3, 1949. Six specimens were taken from cod stomachs at Burwell and three from a bearded seal; the latter were mature, taken northeast of the Gyrfalcon Islands on July 15, 1948. A few, usually small specimens, were caught planktonically at stations 51, towing in shallow water from 0 to 6 metres; 22, towing in the upper 3 metres; 13, towing at 40 metres; 40, towing in the upper 3 metres; 101, at about 6–7 metres; and

228, at the surface. Specimens over 30 mm. long were taken in the dredge, but the only mature individuals were found in the seal and eider duck stomachs.

Anonyx nugax is a circumpolar arctic and subarctic species, confined to fairly shallow water on the shelf, and extending also into the boreal region in the North Sea and Skagerak. It is recorded from Cumberland Sound and Hudson Bay (Shoemaker, 1920) and from the Japan Sea (Derjavin, 1930). Stephensen (1923) has discussed its distribution, breeding cycle and maximum size attained in different parts of its range.

Socarnes bidenticulatus (Bate)

Three specimens were taken: one small immature individual taken pelagically at station 33, one larger immature specimen dredged at station 231, and one mature female, 37 mm. long, at station 203 (July 8, 1950).

An arctic and subarctic species, probably circumpolar, known from south of Newfoundland (Shoemaker, 1930b) but not yet from the Gulf of St. Lawrence, and from the Japan Sea (Derjavin, 1930). It has been recorded from Melville Island (N.W.T.) (Shoemaker, 1920).

Socarnes vahli (Krøyer)

Thirteen specimens, all but one immature, at stations 20, 28, 225, 226 and 231; all taken in the dredge. An almost mature female was taken on August 13, 1950 (station 226). In addition to these thirteen specimens, five were taken in Atlantic cod stomachs at Port Burwell.

The distribution of this species is similar to that of S. *bidenticulatus*, but it extends farther south, especially in Europe, where it is known from southwest Norway. Like the previous species, it is also known from the Japan Sea.

Tmetonyx orchomenoides Stephensen

Three specimens were taken in Ungava Bay, at stations 103 and 234, both on occasions when the one-metre stramin net was allowed to touch bottom, in depths between 80 and 275 metres.

This species, erected by Stephensen (1925), is very close to both *T. cicada* (O. Fabr.) and *T. similis* (O. Sars), distinguished by the produced epistome, the shape of side-plate 4 and the length of per. 5, which is almost as long as per. 6. I have examined the material of all three species in the Copenhagen Museum, and am forced to the conclusion that only breeding experiments could decide whether or not they should be kept separate. Two specimens in the Copenhagen collection marked "*Tmetonyx* (*cicada* O. Fabr.?)—(epistome reaches too far forward; fourth plate posterior expansion deep); SE Greenland, Tasiusarsik 21–7–33" belong to this species, and were probably overlooked by Dr. Stephensen.

The species is known only from southwest and southeast Greenland and Ungava Bay. *T. cicada* is arctic and subarctic, possibly circumpolar, and *T. similis* is known from the Norwegian coast, Iceland, the Faeroes, Scotland and west Svalbard (Stephensen, 1925).

Orchomenella pinguis (Boeck)

Many hundreds of this species, all immature, were taken at station 125A, August 23, 1949, from a seal skull left to be cleaned in 12 metres of water. Sixty-seven specimens, including some mature females, were taken from a shark skeleton similarly treated, in Mission Cove, Port Burwell, on August 8, 1949. Several hundred, including many females close to maturity, came from a beluga skull at station 212 on July 22, 1950, and 23 specimens, many of them ovigerous females, were dredged from 20 metres at station 216 on July 24, 1950. A few immature specimens were caught in plankton nets at stations 22 and 123, in the upper 10 metres in shallow water. One specimen was found in the stomach of a ringed seal at Port Burwell in June 1949.

The last epimer (pleon 3) of *O. pinguis* is, according to Sars (1895), serrate, but Della Valle (1893) describes it as smooth. In specimens from west Greenland in the Copenhagen Museum collection pleon 3 is smooth, as it is in the present Ungava Bay material.

The species has a wide north-south distribution, and is possibly also circumpolar. It is known from the Siberian shelf as far east as longitude 124°E (Brüggen, 1909) and from the Japan Sea (Derjavin, 1930), from the White Sea, the Norwegian coast, and as far south as Mediterranean in Europe and Cape Hatteras in North America (Shoemaker, 1930a). In the Canadian north it has already been recorded from west Hudson Bay (Shoemaker, 1920).

Orchomenella minuta (Krøyer)

Nine specimens were taken. Two females with eggs were caught in the dredge at station 102, June 30, 1949; two immature individuals were dredged at station 216, July 24, 1950; four were collected by hand in the intertidal zone at station 217 July 30, 1950; and one was caught planktonically at station 123, August 10, 1949, in shallow water.

An arctic and subarctic form, circumpolar, and extending down the coast of Norway to the Skagerak, Kattegat and Øresund (Dahl, 1946b), and south on the eastern North American seaboard to Nova Scotia (Shoemaker, 1930a, 1930b). Known from Hudson Bay (Shoemaker, 1920) and also recorded from the Okhotsk Sea (Derjavin, 1930).

Orchomenella groenlandica (H. J. Hansen)

Five immature specimens, all but one approaching maturity, were taken by dredge at station 226, August 13, 1950.

An arctic and subarctic species, known from north Norway and the White Sea (Derjugin, 1928), both coasts of Greenland (Stephensen, 1925), Bay of Fundy and south of Newfoundland (Shoemaker, 1930b).

Family STEGOCEPHALIDAE

Stegocephalopsis ampulla (Phipps)

Syn.: *Phippsia ampulla* (Phipps); Stebbing, 1906.
Stegocephalus ampulla (Phipps); Brüggen, 1909.

One large male specimen of this species was taken in the dredge at station 45, August 23, 1947.

There is disagreement in the literature about the number of joints in the palp of the first maxilla in this species. Brüggen (1909) and Schellenberg (1924) describe it as one-jointed, while Stebbing (1906) and Stephensen (1925) are equally certain that it is two-jointed. After an examination of the present specimen and of the material in the Copenhagen collection from east and west Greenland, it has become clear that the palp in question is open to both interpretations. It is waisted, or constricted in the middle, giving the appearance of two joints although consisting (in my opinion) of only one in fact.

S. ampulla is not a common species. It is predominantly arctic in distribution, but has been taken also in the subarctic. Shoemaker (1920) recorded it for the first time in arctic Canada, at Bernard Harbour. For details of distribution, see Stephensen (1935, 1925, 1933).

Stegocephalus inflatus Krøyer

Three specimens were found in the stomach of a bearded seal, 15 miles ENE of the Gyrfalcon Islands, July 15, 1948. One mature female, with eggs, was dredged at station 103, July 6, 1949.

This is an arctic and subarctic species of wide distribution, circumpolar, recorded from the western, central and eastern arctic of Canada, south on the eastern seaboard to Cape Cod; west and east Greenland, Iceland, Svalbard, west and north Norway, south to the Skagerak; Barents, Kara and Laptev Seas; Plover Bay (east Siberia), Sea of Okhotsk and the Gulf of Tartary (Shoemaker, 1930a) and the Sea of Japan (Derjavin, 1930).

Family AMPELISCIDAE

Ampelisca eschrichti Krøyer

A common species, taken benthonically at stations 20, 45, 102, 107, 201, 203, 126, 216 and 231, in depths ranging from 20 to 130 metres, and planktonically at stations 13 and 18. One specimen came from a cod stomach at Burwell. Mature ovigerous females were taken on July 18, 1947, July 7, 1949, and July 24, 1950.

Stephensen (1935) gives several characters which distinguish this species from *A. macrocephala* Lilljeborg, one of which, the presence of long setae on the lower hind corner of joint 5, per. 7, in the latter but not in the former species, is not valid for the present material. Many of my *eschrichti* possess the long setae, some do not. The two species, however, are easily separated on the shape of the posterior expansion of joint 2, per. 7, and of joint 5 of the same limb. Another good character, which Stephensen does not mention, is that the posterior margin of pleon 3 is far more strongly bisinuate in *macrocephala* than in *eschrichti*.

A. eschrichti is a circumpolar arctic and subarctic species, extending even into the boreal west of the British Isles. In Canada it extends south to the Bay of Fundy and south of Newfoundland, and it has been recorded from Hudson Bay (Shoemaker, 1920, 1926). There is a possibility that it occurs also in the southern hemisphere (Barnard, 1932), or at least that there is a very closely related southern species (Stephensen, 1925). For the northern hemisphere distribution see Stephensen (1933).

Ampelisca macrocephala Lilljeborg

Three specimens of this species were taken in the dredge at station 45 on August 23, 1947. One was an ovigerous female.

The distribution is similar to that of *A. eschrichti*, but the present species extends farther south in the North Sea area. A very closely related form is recorded from the southern hemisphere, possibly the same species (Chilton, 1917). It has been recorded from the Japan Sea (Derjavin, 1930).

Byblis gaimardi (Krøyer)

Altogether 218 specimens of this species were obtained, most of them in the dredge, at stations 45, 102, 107 and 231; 118 specimens were taken in one haul at station 102. The species was also caught in plankton nets at stations 13 and 18, and 77 specimens were found in stomachs of the Atlantic cod at Port Burwell. Ovigerous females were taken on August 23, 1947, and June 30, 1949. There is great variation in the size of the mature females.

The species is probably circumpolar, arctic and subarctic, extending also into the boreal on the Scottish coasts, the North Sea and the Danish Belts. It is also known from Monterey Bay, California (Holmes, 1908) and from South Africa (Barnard, 1916) and Japan (Derjavin, 1930). In eastern North America it is recorded from Jones Sound and northeast Baffin Island (Sars, 1909), Hudson Bay, Labrador, the Gulf of St. Lawrence and the New England coast (Shoemaker, 1930a). For details see Oldevig (1917) and Stephensen (1935).

Haploops tubicola Lilljeborg

One hundred and eight specimens were taken, all benthonically, at stations 45, 102, 106, 201C and 231. Ovigerous females were taken on July 7, 1949, and June 29, 1950.

A circumpolar arctic, subarctic and boreal species, ranging south to the Mediterranean. Known from the Gulf of St. Lawrence and the Bay of Fundy (Shoemaker, 1930a) and recorded from depths down to 1200 metres in the Norwegian Sea (Sars, 1885). Also known from the Californian coast and the Sea of Japan (Derjavin, 1930).

Haploops setosa Boeck

Syn.: *Haploops robusta* G. O. Sars. **New Synonymy.**

Altogether 466 specimens were taken, all but five of them in stomachs of Atlantic cod at Port Burwell during the 1947, 1948, 1949 and 1950 seasons. One individual was taken in the dredge at station 30 and two in plankton nets at station 41, towing at about 230 metres close to the bottom, and at station 103, towing close to the bottom in 92 metres. Two specimens came from the stomach of a ringed seal at Burwell.

Haploops setosa is here combined with *H. robusta*. Sars's species (*robusta*) was erected on a single specimen taken off the coast of Finmark (Sars, 1895) differing from *setosa* in larger size, more robust form, evenly rounded lateral corners of the cephalon, shorter antennae, the shape of pleon 3, which was more rounded and with less marked pointed production at the corner, by the slightly shorter expansion of joint 2, per. 7, shorter second joint in the peduncle of antenna 1 and a deeply cleft telson. Shoemaker (1931), discussing material from the Bay of Fundy, writes: "I believe that *H. robusta* is but a large form of *H. setosa*, but have hesitated to place it in synonymy for want of authentic speci-

mens of *H. robusta* with which to compare my material". Norman (1900a) expressed similar doubts about the same material.

Most of the Ungava Bay specimens are large, from 25 to 27 mm. in overall length, and they cannot be referred without reservation and qualification to either species, having characters of both, as the two are described in the European literature. Nor would it be at all proper to describe a new species. The solution, therefore, is to place the two species in synonymy, the species being then represented by geographic variants in different parts of the range; possibly the Ungava Bay population represents a hybrid form, or (more probably) the common ancestor of the two European variants. The same procedure is proposed below for another pair of European species, *Westwoodilla caecula* and *W. megalops*, which presented the same problem when compared with the Ungava Bay material.

The Ungava Bay specimens, some of which are mature, show lateral cephalic corners that are distinctly quadrate, a character of *setosa* Boeck; the telson, however, is cleft almost to the base, a character of the *robusta* form; joint 2, per. 7 reaches to halfway along joint 4, resembling *setosa*; the hind margin of pleon 3 is rounded and only very slightly produced at the corner (*robusta*); joint 2 of the peduncle of antenna 1 is much longer than joint 1 (*setosa*); and the large size is a character of the *robusta* of Sars.

In point of fact, the two forms are very close even within north-western Europe. Stebbing (1894) describing specimens of *robusta* from the Barents Sea, says that the angles of the head "are not so strongly rounded off as in Sars's figure, but more so in some specimens than others. The angles of the third pleon segment are minutely produced, at least in some of the specimens including the largest. The proportions of the antennae do not differ much from those of *Haploops setosa* . . . The telson is much more deeply divided then in *Haploops setosa*. In the fifth peraeopods the fourth and fifth joints are rather longer in proportion to their breadth than in the species just named, but with all the differences allowed for, the resemblance between the two species remains extremely close". Stephensen (1925) described a specimen of *robusta* from west Greenland (the only specimen from that whole coast referred to that species) as differing from Sars's original description "in having a tooth at the hind corner of the epimeral part of the 3rd metasome segment", a variation resembling the *setosa* pattern.

I have not seen any European specimens of *H. robusta* Sars, nor the Greenland specimen just mentioned. Judging from the statements of Stebbing (1894) quoted above, the two are close together in Europe, but not identical; and they apparently do not show the mixture of distinctive characters described here for the Ungava Bay specimens. The nomenclatural problem raised is the same as in the case of the species of *Westwoodilla* already mentioned (see below) to which discussion the reader is referred. With the addition of the Ungava Bay material and the extension of range involved, the two European forms must be regarded as of subspecific rank or as geographic variants and not as full species.

Haploops setosa Boeck has not so far been taken east of the Kara Sea nor

west of Ungava Bay, and it may therefore be of strictly Atlantic origin. It has been taken in the subarctic from the Kara Sea, Barents Sea, Iceland and west Greenland, and also in the arctic region in Scoresby Sound and Franz Joseph Fjord, and in the boreal waters of Scotland, the Faeroe-Shetland Channel and southwest Norway, usually in deep water. *H. robusta* Sars is known only from the Barents Sea, west Greenland (Nordre Strømfjord, one specimen only) and from the Bay of Fundy.

Family HAUSTORIIDAE

Pontoporeia femorata Krøyer

Only one specimen of this species was taken, an immature individual caught in a plankton net towing at the surface at night, station 125, August 21, 1949.

The species is circumpolar, arctic and subarctic, usually found in shallow water. A presumably relict population is present in the Baltic Sea. It has already been recorded from northern Canada in Jones Sound and northeast Baffin Island (Sars, 1909) and in James Bay (Shoemaker, 1926), and it is known from the New England coast (Holmes, 1905) and from the Japan Sea (Derjavin, 1930; Yashnov, 1948); New Siberian Islands (Brüggen, 1909), Kara Sea (Stuxberg, 1882), Laptev Sea (Gurjanova, 1932), Bernard Harbour (Shoemaker, 1920).

Pontoporeia affinis Lindström. (Fig. 5)

Twenty-two specimens are in the collection, all taken in plankton nets, at stations 1 (hauling at 5 metres), 31 (surface haul), 44 (hauling at about 80 metres) and 51 (upper 5 metres). All but station 44 are in regions of strong freshwater influence, and since closing nets were not used it is impossible to tell at what depth the specimen at station 44 was actually caught. A mature ovigerous female was taken at station 51, on August 5, 1947.

The telson (Fig. 5) is not broader than long as described in the older European literature; it is leaf-like, each half ovally rounded. The pleon is not hirsute, again in contrast to the European freshwater specimens. This is in

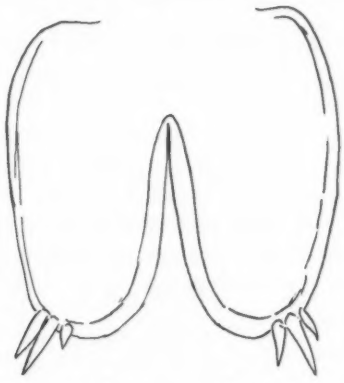

FIGURE 5. *Pontoporeia affinis*, telson.

agreement with the general rule of loss of sensory hairs as the environment becomes more saline, found to a very high degree, for instance, in the species of the genus *Gammarus*. The genus has recently been revised by Segerstråle (1937) who has reduced the number of species to two, *affinis* and *femorata*, the former embracing several earlier species including the North American freshwater forms *P. filicornis* Smith and *P. hoyi* Smith. The largest specimen in the Ungava Bay material measures 14 mm., which is 3 mm. longer than the maximum iength given by Segerstråle (1937) for arctic specimens.

P. affinis was taken by the Canadian Arctic Expedition at Collinson Point, Alaska (Shoemaker, 1920) in very shallow water, and it is known (following Segerstråle's revision) from numerous freshwater lakes in Canada and the northern United States (Larkin, 1948). The present records from Ungava Bay, however, appear to be the first for the eastern seaboard and the Canadian eastern arctic, in salt water. It is a widespread species in the north but not circumpolar, often found in brackish regions such as the mouths of the Siberian rivers (Yashnov, 1948) and it is known as a glacial relict in freshwater in Europe and Asia as well as in North America. It does not appear to have been recorded from Greenland. For a more detailed account of its distribution see Stephensen (1938). It is probably of Pacific origin.

Family AMPILOCHIDAE

Gitanopsis arctica G. O. Sars

Two females of this species were taken in the stramin net at station 18, towing at depth of about 50 metres on July 17, 1947.

The species has not often been found; the known localities so far are: North Norway (Varangerfjord; Sars, 1895), east of Iceland, southwest Greenland (Bredefjord; Stephensen, 1925), southern Novaya Zemlya (Stappers, 1911) and now Ungava Bay.

Family STENOTHOIDAE (including METOPIDAE)

Metopa sinuata G. O. Sars. (Fig. 6)

Three females were dredged at station 210, July 21, 1950, and one male and one female at station 226, August 13, 1950.

This species is close to both *M. bruzelii* and *M. propinqua*. It is separated from *bruzelii* by the sinuous side-plate 4, shorter antennae, slightly longer projection downwards of joint 4, per. 6 and 7, and the serrate palm of the second gnathopods (per. 2), which otherwise closely resemble the second gnathopods of *bruzelii* (Fig. 6). It is closer still to *M. propinqua*, and it is not possible always to be certain of the determination of the females (the males are easily separated by the different form of the sixth joint of per. 2 (see next species)). In the female the palm of per. 2 is somewhat more sloping than in *propinqua* and there are two pairs of spines on the telson (three in *propinqua*). Spines on the telson are variable characters in many amphipod species, and they cannot be

considered reliable characters. The shape of joint 4, per. 6 and 7, which is used by Sars (1895) and Stebbing (1906) to separate the two species (straight hind margin in *sinuata*, curved in *propinqua*) does not seem to be a useful character in the present material, nor for the Greenland specimens examined in the Copenhagen collection; the hind margin is curved to about the same degree in both species. The lower margin of side-plate 4, however, does show a slight but recognizable difference, being more obviously sinuate in *sinuata* than in *propinqua*. The antennae in the present specimens, and also in the Greenland (Copenhagen) material, are slightly longer than figured and described for this species by Sars (1895).

This is a subarctic species which has been recorded also from one arctic station (Scoresby Sound–Stephensen, 1931, 1944a) and from the Norway–Faeroe–Scotland area just south of the subarctic proper. It is probably a species of the Atlantic subarctic and not of the Pacific side, being known from many localities in west Greenland, Svalbard and Franz Joseph Land, but not recorded from the Siberian coast or from the Bering Sea region. It is here recorded for the first time from North America.

FIGURE 6. *Metopa sinuata*, per. 2, female.

Metopa ?propinqua G. O. Sars. (Fig. 7)

Two males and one female were dredged at station 226, August 13, 1950.

The determination is not quite certain, but the differences between these specimens and the typical *propinqua* may be due only to local variation. The male was not described by Sars (1895), but male specimens from the Barents Sea were referred to this species by Brüggen (1909), who gave a figure of the

only important difference from the female, namely the form of joint 6, per. 2. My two male specimens show precisely the same form of per. 2 (Fig. 7) and are in agreement in all other characters except in the relative lengths of the antennae. In Sars (1895) the anterior antennae of the female are described as slightly longer than the posterior antennae. In the female specimen from Ungava Bay the anterior antennae are slightly shorter, and they are much shorter in the males, as shown in Figure 7. Brüggen gives no information on the relative length of the antennae in his specimens, which have not been available during the present study; he says that the "antennae are longer, about three quarter the length of the body", which applies also to the second antennae of the present specimens but not to the first. Brüggen describes the anterior margin of joint 5, per. 2, as "sehr fein gesägt"; there are in fact several rows of very small tubercles

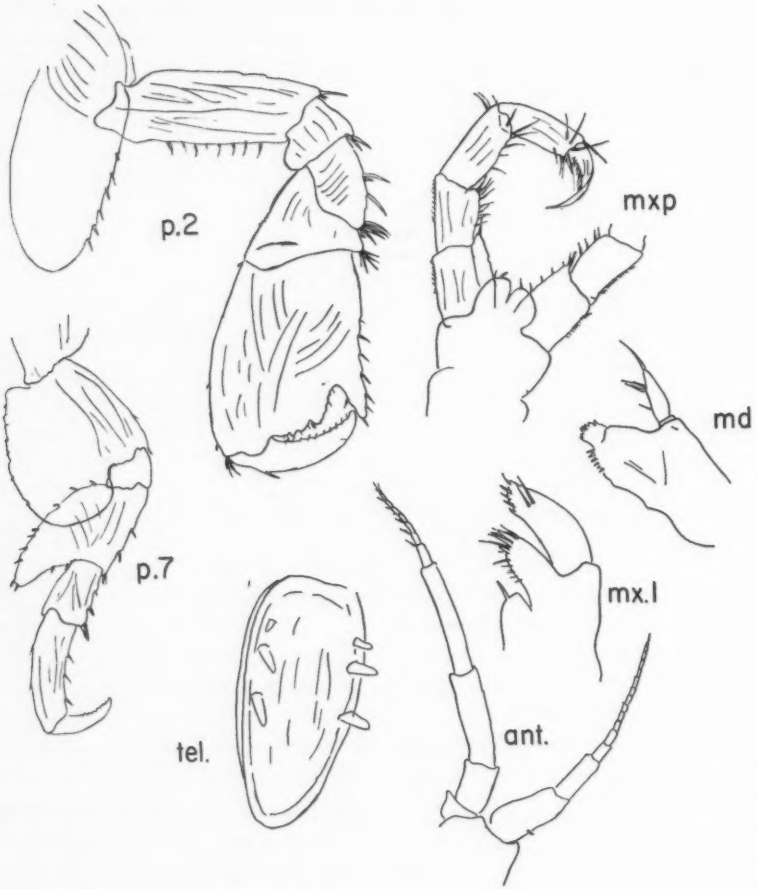

FIGURE 7. *Metopa ?propinqua*, male.

on the joint in question, one of which appears in profile when seen from the side.

In view of the acknowledged complexity and variability of the family Stenothoidae, and especially of the genus *Metopa*, it is wiser to refer these specimens to *propinqua*, with appropriate notes of differences, than to describe a new species or even subspecies. It will be noted that there are rudimentary, or vestigial, outer plates in the maxillipeds, and that the expansion of joint 2, per. 7, is similar in the two sexes but more strongly formed in the male. The third joint of the mandibular palp is missing and the first joint is very small, almost vestigial.

The larger of the two males measures 4.25 mm., over one millimetre longer than the length given for the female (Stebbing, 1906). It is subarctic and boreal in distribution, known from the Barents Sea and northern Norway, the North Sea, Firth of Forth and Bohuslän (Oldevig, 1933), and the Gulf of St. Lawrence (Shoemaker, 1930a). The latter record was the first in North America.

Metopa bruzelii (Goës)

Thirteen specimens, all females, were taken in the dredge at stations 210 and 226, on July 21 and August 13, 1950. Mature females were taken at both stations.

The projection of joint 4, per. 6 and 7, is longer than described and figured by Sars (1895), extending almost to the end of joint 5. Stebbing (1906) describes it as "below the middle of the 5th". Specimens from Greenland in the Copenhagen collection show variation in the length of this joint, sometimes to the end of the fifth, in agreement with the Ungava Bay specimens.

Stebbing (1906) put this species in the genus *Proboloides*, in the belief that the first maxilla had a two-jointed palp. (It is doubtful whether the sturdy reliance on the mouthparts shown by the classical amphipod systematists gives a true natural classification.) Stephensen (1926) put the species back in *Metopa*, where it belongs, commenting on the shift and stating that his *bruzelii* had one-jointed palps in the first maxillae, as have the present specimens from Ungava Bay.

This is an Atlantic subarctic species, extending both south into the boreal (British Isles, Norman, 1900b) and north into the arctic (Smith Sound, Sars, 1909); Norway, Skagerak (Enequist, 1949), Faeroes, Iceland, west Greenland and the Gulf of St. Lawrence (Shoemaker, 1930a).

Metopa cariana Gurjanova. (Fig. 8)

The collection includes 20 specimens of this species, new for North America. Two were taken in plankton nets at stations 13 and 44; the remainder were dredged at stations 203, 226 and 231. One mature ovigerous female was taken on August 7, 1950.

Metopa cariana is known from the Kara Sea, the Sea of Japan (Gurjanova, 1929, 1938), northeast Greenland (Schellenberg, 1935), southeast Greenland (Stephensen, 1944a) and now from Ungava Bay. It is extraordinarily close to *Proboloides glacialis* (Krøyer), and if, as I suspect, the two species are synonymous, in which case the name should be changed to *Metopa glacialis* (Krøyer), the distribution would include records of *P. glacialis* from the White Sea, west Greenland, Iceland, Svalbard and Norway (Stephensen, 1931, 1938).

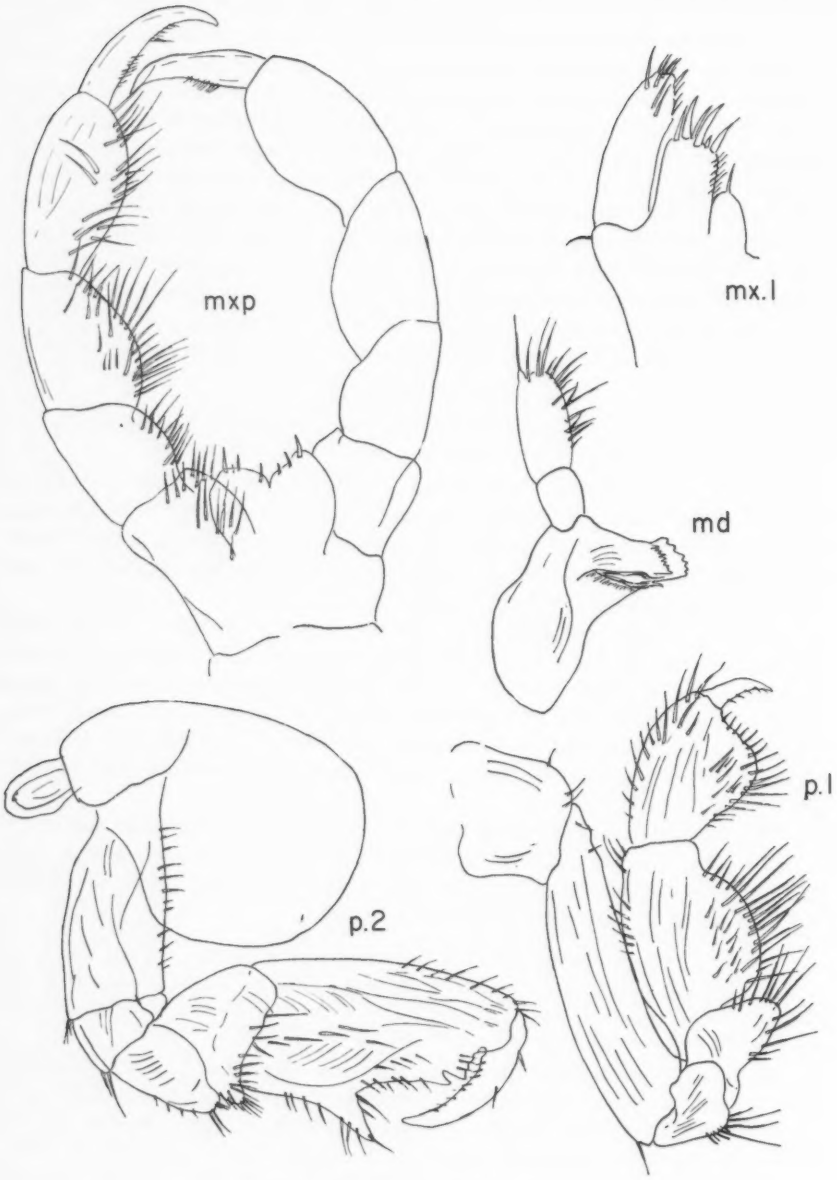

FIGURE 8. *Metopa cariana.*

The present species was established in a very short description (Gurjanova, 1929) with figures of the gnathopods, telson and last uropod. The palp of the first maxilla is described as one-jointed, and the inner plates of the maxillipeds as being fused together. In both these characters the present specimens are in agreement, placing them firmly in the genus *Metopa* as at present defined. Schellenberg (1935), however, describes specimens from Franz Joseph Fjord as having the inner plates of the maxillipeds separate, "fast bis zum Grunde gespalten". Schellenberg also points out that the only significant difference between this species and *Proboloides glacialis* (Krøyer) lies in the one-jointed palp of the first maxilla (two-jointed, according to the literature, in *Proboloides*). That two forms, otherwise identical, should be separated not simply into two species but into two genera, on the basis of the number of joints in maxillary palp, is contrary to the very foundations of systematics and zoogeography. Unfortunately "*Proboloides glacialis*" has not been taken often and there is no specimen in the Copenhagen collection that has the first maxillae intact; the preparation of the first maxillae of the type specimen has deteriorated to such an extent that it is no longer possible to decipher their structure. The question of the possible identity of *glacialis* and *cariana* must therefore be left in abeyance for the time being.

Metopa alderi (Sp. Bate). (Fig. 9)

Syn.: *M. spectabilis* G. O. Sars.

In putting these two species together I am following Dahl (1946a) who has shown that in specimens from the North Sea, Skagerak and Kattegat it is impossible to distinguish them statistically on a variety of measurements, and that the only real difference between the smaller form (*alderi*) and the larger (*spectabilis*) is the time of onset of maturity, a matter which appears to be controlled by the temperature of the water. Three mature females, with eggs, taken at station 226, August 13, 1950, referred to the smaller *alderi* type, measured 5.0, 6.5 and 6.5 mm. Sixteen of the *spectabilis* type were taken at stations 103 (July 6 and 8, 1949)

FIGURE 9. *Metopa alderi*, per. 2, male.

and 226 (August 13, 1950), of which the mature specimens measured 8.75, 10.25, 11.75, 12.0, 13.0, 13.0, 14.5, 14.5, 15.0, 15.0, 15.25, 15.5, 17.0 and 17.5 mm. These figures suggest a bimodal distribution, but the number of measurements is very small. Since the species is quite frequently taken planktonically it is not impossible that we have here a size-distribution of the same sort as is known in the Calanoid *Calanus finmarchicus* and other copepods in Greenland waters, which may be related to development in two different types of water, polar and Atlantic. Enequist (1949) keeps *alderi* and *spectabilis* separate, without however answering the evidence offered by Dahl for their unification.

The Ungava Bay specimens show one constant variation from type, in the form of the palm of the sixth joint of per. 2 in both sexes. The bight in the palm, which is more marked in the male than in the female, is partly filled in, when compared with the typical form (Sars, 1895; Stebbing, 1906), by the development of one or more small additional lobes, as shown in Figure 9. Specimens in the Copenhagen collection, from the *Ingolf* Expedition station 31 (66°35′N, 55°54′W), show the same variation, but five specimens taken in the Skagerak in November 1952 showed the typical pattern. The variant is possibly a western Atlantic form.

The species is known in the *alderi* form from west Svalbard, the Murman coast, White Sea (Yashnov, 1948), north Norway, east Greenland, southwest Iceland, Bohuslän and the coast of Wales; in the *spectabilis* form from north Norway and the deep water of the Norwegian Sea, the Kara Sea, southeast Svalbard, Skagerak and Kattegat, North Sea, west Greenland and the Gulf of St. Lawrence. It is thus predominantly a subarctic species, extending both north and south of the subarctic zone proper.

Metopa longirama Dunbar. (Fig. 10)

Two specimens, one male and one female, were taken planktonically at station 9, on July 11, 1947, towing at approximately 15 metres.

The original specimen of this species (Dunbar, 1942) was also taken in the plankton. The original description is adequate for the recognition of the species, with the following addition: The coxal plates were described as "similar to

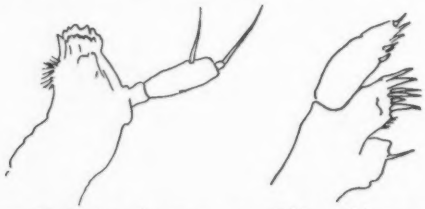

FIGURE 10. *Metopa longirama*, mandible and first maxilla.

M. alderi"; this should be amended to the extent of noting that side-plate 4 is a little smaller than in *alderi*. Pleon 3 is almost quadrate, slightly less than a full right angle. Figures of the mandible and first maxilla, which were slightly damaged during dissection in the type specimen, are given here (Fig. 10).

The species is known so far only from Clyde River (Baffin Island) and Ungava Bay.

Metopa norvegica (Lillj.). (Fig. 11)

Seventeen specimens were taken in the plankton at station 18 and five were dredged at stations 103 and 106. One of these was a mature female, taken on July 6, 1949.

This material shows the changes which take place in the second gnathopod (per. 2) during the life of the individual. The deep notch in the palm, a diagnostic character of the species, is not present in the small immature specimens at all; the palm is almost straight, at right angles to the hind margin, and almost smooth. The beginning of the appearance of the notch is shown in Figure 11, drawn from a young female with small brood lamellae. The shape of the notch at the next moult stage following the stage at which the individual was caught, in which the notch is much deeper, can also be seen in the drawing.

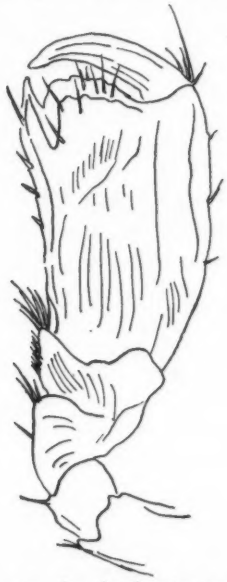

FIGURE 11. *Metopa norvegica*, immature female, showing two moult stages in the development of the palmar notch of per. 2.

This is apparently another Atlantic subarctic species, not so far recorded from the Pacific or Siberian side. It is known from the White Sea and the Murman coast, north and west Norway, west Greenland, Iceland and the Faeroes; North Sea and off St. Ives in Cornwall; Skagerak (Stephensen, 1931, 1938). It has not hitherto been reported from North America.

Metopa nordmanni Stephensen. (Fig. 12)

Three specimens in all, a male and a mature female at station 226, August 13, 1950; a mature female at station 210, July 21, 1950.

These specimens have been carefully compared with the type specimen in the Copenhagen Zoological Museum. The distinctive features are the shape of

FIGURE 12. *Metopa nordmanni*, per. 2 from two different individuals.

joint 6, per. 2, and especially the palm (Fig. 12), the rather square lower margin of side-plate 3, and the length of joint 5, per. 1 (longer than in most *Metopa* species, but not as long as in *M. leptocarpa* G. O. Sars).

The species is known so far only from three subarctic localities—west Greenland (Nordre Strømfjord, the type locality (Stephensen, 1931), the Kara Sea, or more accurately Yugorskii Shar (Gurjanova, 1935a, 1935b; Yashnov, 1948), and Ungava Bay.

Metopa longicornis Boeck

Three specimens, two from station 226 and one from stations 103. A female taken at the former station on August 13, 1950, was almost mature. This specimen has two pairs of spinules on the telson, not three as in the original description and as figured by Sars (1895). The male taken at station 103 has three pairs.

The species is known from west Greenland (Stephensen, 1931), Laptev Sea (Yashnov, 1948) and Norway (Sars, 1895). This is the first North American record.

Metopa invalida G. O. Sars

Taken at station 226, August 13, 1950; 22 mature females. This particular dredge haul was very rich in Metopids, and many immature specimens and males have not been sorted out for identification.

As this species has never been recorded hitherto since its original description from Hammerfest and Selsøvig (Sars, 1895), the identification was carefully checked against specimens from Sars's original material from Selsøvig in the Copenhagen collection, with which the present specimens agree in all details. In the Copenhagen material there is the same variation in the length of joint 4, per. 6 and 7, as in the Ungava Bay specimens; in some the projection reaches almost to the end of joint 5. The long and unarmed telson is especially distinctive.

*Metopa **hearni*** n. sp. (Fig. 13)

Five females, some of them mature, were dredged at station 210, July 21, 1950; one mature female was taken at station 226, August 13, 1950, together with other species of the same genus; and one immature specimen (male?) was taken at station 102, June 6, 1949.

Body rather compressed. Head, lateral corners produced, bluntly pointed. Side-plates deep, fourth side-plate large and a little deeper than broad. Pleon 3 produced, bluntly acute. Eyes round, medium in size. Antennae short, equal. Antenna 1, first joint of peduncle equal to second and third together. Antenna 2, joints 4 and 5 of peduncle equal. Mouthparts normal for the genus, but first joint of mandibular palp very small, evanescent, third joint missing. Per. 1 stout, short, joint 5 about three-quarters of joint 6 in length. Per. 2 fairly heavy, hand (joint 6) broad, palm well defined by two spines at the angle, smooth. Per. 3 and 4 rather long, slender, per. 5–7 of medium weight, posterior process of joint 4 reaching to end of joint 5 on per. 6 and 7, not so far on per. 5. Per. 5, joint 2 linear; expanded in per. 6 and 7. Telson almost oval, unarmed. Length 3 to 4 mm. The species is named after Hearn, after whom Hearn Island, Diana Bay, is named.

This species is fairly close to *M. invalida* G. O. Sars, but differs in the broader and more rounded telson, the more acute pleon 3, the longer projection of joint 4, per 6 and 7, and the shape of per. 1 and 2. The distinctive spine on the posterior margin of joint 6, per. 1, of *invalida* is not found in *hearni*. The type (No. MJD–001) and cotypes are deposited in the Redpath Museum, McGill University. The type specimen comes from Station 210, July 21, 1950.

Metopella nasuta (Boeck)

One mature female, with eggs, was taken in the stramin net at station 18, July 17, 1947. The net touched bottom during the haul.

The species is known from north and west Norway, Skagerak, Scotland, southeast Iceland, southwest Greenland and the Gulf of St. Lawrence.

Metopella neglecta (H. J. Hansen)

Four specimens were taken; in the benthos at stations 226 and 210, and in the plankton at station 5, towing at about 20 metres. The latter specimen, taken on July 27, 1948, is mature.

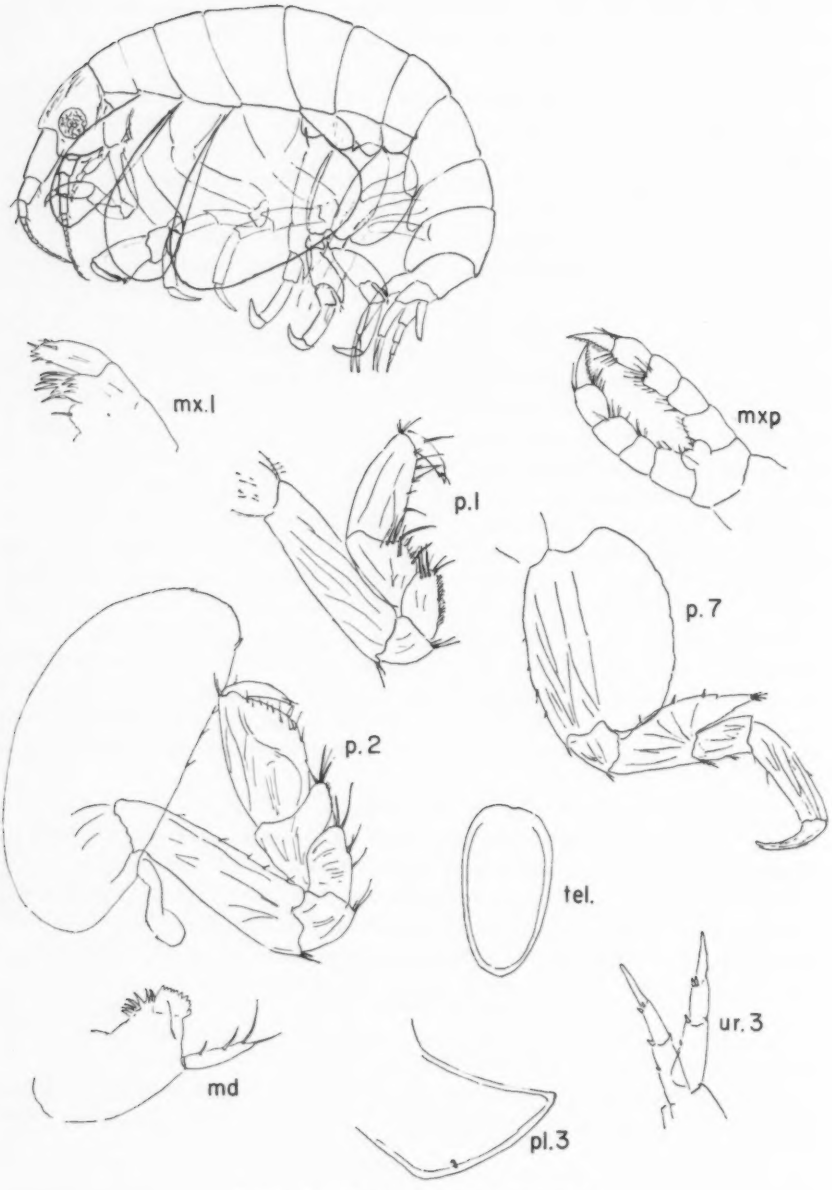

FIGURE 13. *Metopa hearni* n. sp., female.

The species is known from Franz Joseph Land, west Norway (Haugesund) and west Greenland. This appears to be the first record for North America.

Metopella carinata (H. J. Hansen)

Altogether 14 specimens of this species were obtained, all in the plankton, at stations 33 (towing at 10 metres), 40 (towing at 2 metres) and 123 (towing in the upper 5 metres). Mature ovigerous females were caught at the latter station, August 10, 1949.

This species is arctic and subarctic, known so far only from Greenland and eastern Canada: west Greenland, from Umanak southward; east Greenland, near Angmassalik; Canada, Gulf of St. Lawrence, Ungava Bay (present records) and Jones Sound, southwest Ellesmere Island.

Metopella longimana (Boeck)

Six females of this species were dredged at stations 103, 210 and 226; ovigerous specimens at the latter station only, August 13, 1950.

The species is known from west Greenland, from Egedesminde to the Julianehaab district, from Angmassalik in east Greenland, from northeast Iceland and west Norway (Oslofjord and Haugesund) (Stephensen, 1931). This is the first record for North America.

Stenothoe brevicornis G. O. Sars, var. ***canadensis***, n. var. (Fig. 14)

Three ovigerous females and two males were taken at station 226, August 13, 1950.

Like *Metopa invalida*, above, this species has not hitherto been recorded elsewhere than at the Norwegian coast (Hardangerfjord, Bekkervik, Trondheimfjord). In the Ungava Bay specimens there are a few small variations from the

FIGURE 14. *Stenothoe brevicornis* var. *canadensis*, n. var.; per. 2, female.

Norwegian originals which justify the establishment of a new variety, as follows: Head, lateral corners rounded, not "obtusely angular" (Sars, 1895); side-plate 3, not distally widened, sides almost parallel; per. 2, angle of palm is hardly

produced at all (Fig. 14); uropod 3, peduncle unarmed, not provided with "five very minute denticles", as described by Sars. Otherwise the Ungava Bay specimens agree with Sars's description and figures.

Family ACANTHONOTOZOMIDAE

Odius carinatus (Sp. Bate)

One small specimen was dredged at station 103, and a larger specimen, apparently an immature male, was taken at station 226.

This is predominantly a subarctic form, like many such species found also in west Norway and the North Sea. It has been recorded also from the Bering Sea (Holmes, 1910). Known from west Svalbard, White Sea, Skagerak and the Northumbrian coast, west Iceland and west Greenland. This is the first recorded find in the waters of eastern North America.

Acanthonotozoma serratum (O. Fabr.)

One immature specimen was taken in the plankton at station 13, towing at 40 metres; another came from the dredge at station 33, and one was taken in the stomach of an Atlantic cod at Port Burwell.

This is an arctic and subarctic (panarctic) species of wide depth range, known from the New Siberian Islands (Yashnov, 1948), the Kara Sea and west to Cumberland Sound in Baffin Island, from northern Svalbard to the Skagerak, Jan Mayen, Iceland, northeast and west Greenland, southern Labrador and the Bay of Fundy. It has been taken in the Norwegian Sea at 753 metres; the other records are from shallower water.

Acanthonotozoma inflatum (Krøyer). (Fig. 15)

Two specimens, a male and a female, were taken, the male at station 18, in a stramin net which touched bottom, the other in the dredge at station 58 on July 28, 1948. The female has well developed oostegites, but there is clearly at least one more moult to come before maturity.

The male agrees well with the full description and figures given by Stebbing (1894), but the female differs in the shape of the first four coxal plates. Plates 1 to 3 are less sharp than in Stebbing's description and plate 4 lacks the second emargination of the posterior edge. The claws (joint 7) of per. 1 and 2 have fewer teeth than shown and described by Stebbing. Per. 1, 2 and 4, with their coxal plates, are shown in Figure 15. Since in all other characters the specimen agrees with Stebbing, the differences illustrated can probably safely be ascribed to immaturity.

This an arctic and subarctic circumpolar species, not yet taken in Iceland. It is known from the Laptev and Kara Seas (Gurjanova, 1936a), White Sea, Svalbard, Barents Sea, Labrador and the Gulf of St. Lawrence, northeast Greenland (Schellenberg, 1935), west Greenland and Baffin Bay. There is a station in Hudson Strait on the chart of distribution published by Stephensen (1931) for which I have been unable to find the authority. The species has also been reported from Collinson Point, Alaska (Shoemaker, 1920).

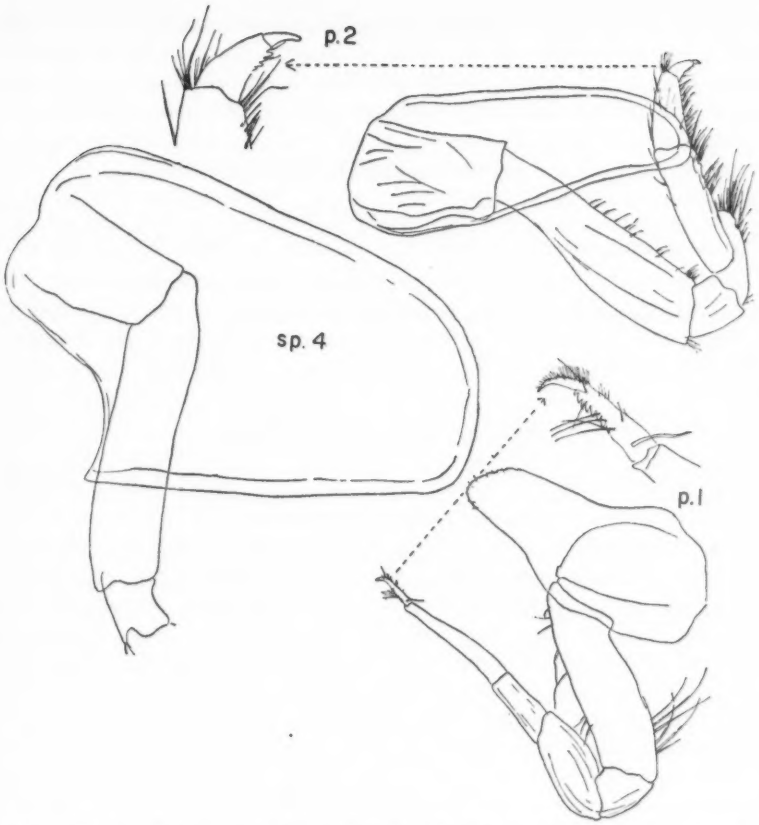

FIGURE 15. *Acanthonotozoma inflatum*, female with well developed brood lamellae, but not quite mature.

Family PARDALISCIDAE

Pardalisca cuspidata Krøyer

Eight specimens in all, six taken in the plankton at station 13, towing at 40 metres; one taken in the stramin net at station 18 when the net touched bottom, and one taken in the dredge at station 234. All specimens are immature.

There are certain small variations from the figures and description in Sars (1895), owing to the immaturity of the specimens. In particular, the spination of the telson is less than in the adult and the subdorsal lobes on metasome segment 3 are rounded, not sharp as in the adult. In these differences the Ungava Bay specimens agree with specimens in the Copenhagen collection from Lindenowfjord, southeast Greenland, which are also immature.

This is an arctic and subarctic species, found both in the plankton and benthonically at depths down to 550 metres (Norwegian Sea). It is known from

the Laptev Sea (Gurjanova, 1935a), Kara Sea, Murman coast, White Sea, Franz Joseph Land and Svalbard, the coast of Norway down to the Skagerak, the Faeroes, Jan Mayen, Iceland, northeast and southeast Greenland, west Greenland and the Gulf of St. Lawrence (Stephensen, 1944a; Shoemaker, 1930a).

Family OEDICEROTIDAE

Oediceros saginatus Krøyer

Ten immature specimens were taken in the plankton, at stations 1, 9, 40 and 124.

The species is known mainly from the subarctic, but three records (northeast Greenland, northeast Baffin Island and the Siberian coast close to East Cape (Stuxberg, 1882)) are arctic. Otherwise known from Jugor Strait, Barents Sea, Svalbard, north and west Norway, west Greenland and Hudson Bay (Shoemaker, 1926).

Paroediceros lynceus (M. Sars)

Twenty-four specimens, all immature, were taken in Ungava Bay, planktonically at stations 1, 18, 13, 101, 123 and 124, and in the benthos at stations 45, 102, 201 and 203. Five specimens were found in Atlantic cod stomachs at Port Burwell.

This species has already been recorded from the eastern arctic of Canada, in Jones Sound (Sars, 1909) and the east coast of Baffin Island (Ohlin, 1895). It has also been taken already in Ungava Bay, at Burwell (Shoemaker, 1920). Probably circumpolar arctic and subarctic, it is known from the Siberian coast as far east as longitude 173°W (close to East Cape) (Stuxberg, 1882), from the Japan Sea (Gurjanova, 1938), Alaska (Shoemaker, 1920) and south in the Atlantic area to New England (Holmes, 1905), Cape Farewell, Iceland and northwestern Norway; Kara and Laptev Seas (Gurjanova, 1932, 1935a).

Arrhis phyllonyx (M. Sars)

Four immature specimens were dredged at station 201, June 29, 1950.

This is a circumpolar arctic and subarctic species, known from the New Siberian Islands and from the Canadian central arctic (Dolphin and Union Strait (Shoemaker, 1920)), and from many arctic and subarctic stations in the Atlantic sector. See Stephensen (1931) for chart of distribution in this sector, and (Stephensen, 1944a) for east Greenland records. It has already been taken in the eastern arctic (northeast Baffin Island (Ohlin, 1895)) and it is known from the Gulf of St. Lawrence (Shoemaker, 1930a).

Westwoodilla brevicalcar (Goës)

Three immature specimens, one a juvenile male, were taken in the plankton at stations 101, 123 and 124, towing between the surface and 10 metres.

The identification has been checked against specimens in the Copenhagen collections. The curvature of the second joint of the mandibular palp is not so striking as is figured by Sars (1895) for the genus, and as implied by Stebbing (1906) in the generic description. This applies also to the next species below, and has been confirmed by examination of specimens of both species in the Copenhagen material. The present species of *Westwoodilla* are very close

together morphologically (see below); *brevicalcar*, in eastern Canadian arctic and subarctic waters, is separable from *megalops* and *caecula* only on the slightly larger size of per. 1 and 2, and the sharper frontal process of the head.

The species is apparently subarctic, recorded from Svalbard, the Barents Sea, northwest Norway, southeast Iceland, west Greenland, Hudson Strait and the Gulf of St. Lawrence. It has not been taken outside the Atlantic subarctic region, and its distribution fits closely the definition of the subarctic marine region employed in the present series of papers (see above, introduction).

Westwoodilla megalops (G. O. Sars). (Fig. 16)

Syn.: *W. caecula* (Bate) (*Halimedon mülleri* Boeck and *Westwoodilla hyalina* Stephensen, 1926). **New synonymy.**

Eleven specimens were taken in the stramin net at station 18, on July 17, 1947. The net touched bottom during the haul.

The fusion of *W. megalops* and *W. caecula* is here proposed on the grounds that it is impossible to place the present specimens, and specimens from the Gulf of St. Lawrence (see below) in one species or the other, characters of both forms being present. The two species were originally described from European (Norwegian) specimens, and it is clear from European work that the population can be separated into two in that region. It apparently cannot be split into two in North America. Three possible solutions to the resulting taxonomic problem appeared to be available: (1) to leave *W. megalops* and *W. caecula* as full species and to make a new species on the present specimens from Ungava Bay; (2) to place *megalops* and *caecula* in synonymy for the North American seaboard only, which would be a departure from nomenclatural practice; (3) to place all three forms in synonymy, with or without the use of subspecific names. The obvious identity of the present specimens with the *megalops-caecula* group in Europe made the first possibility inadvisable, and the second solution might lead only to confusion. I have therefore decided to place all three in synonymy, without using subspecific names to distinguish them. Individuals may be referred to as belonging to the "*megalops*" or "*caecula*" form, or populations may be distinguished geographically. According to Stephensen (1931) the *caecula* form dominates in the southern part of the range in west Europe (Kattegat, Skagerak, North Sea) while *megalops* dominates in the northern part (northwest Norway, Iceland and Greenland).

Stephensen (1931), who kept the two forms distinct as species as the result of study of European specimens, showed that his specimens of the two forms from Norway and Denmark could be separated on the following characters:

W. megalops	*W. caecula*
Telson transversely truncated or slightly emarginate	Telson oval, evenly rounded
Joint 2, per. 7, upper hind corner rectangular with rounded point. Margin sparsely setose	Joint 2, per. 7 evenly rounded, "making part of a circular arch". Margin densely setose
Antennae shorter	Antennae longer
Body form in female stout (slender in male)	Body form in female slender (slender in male)

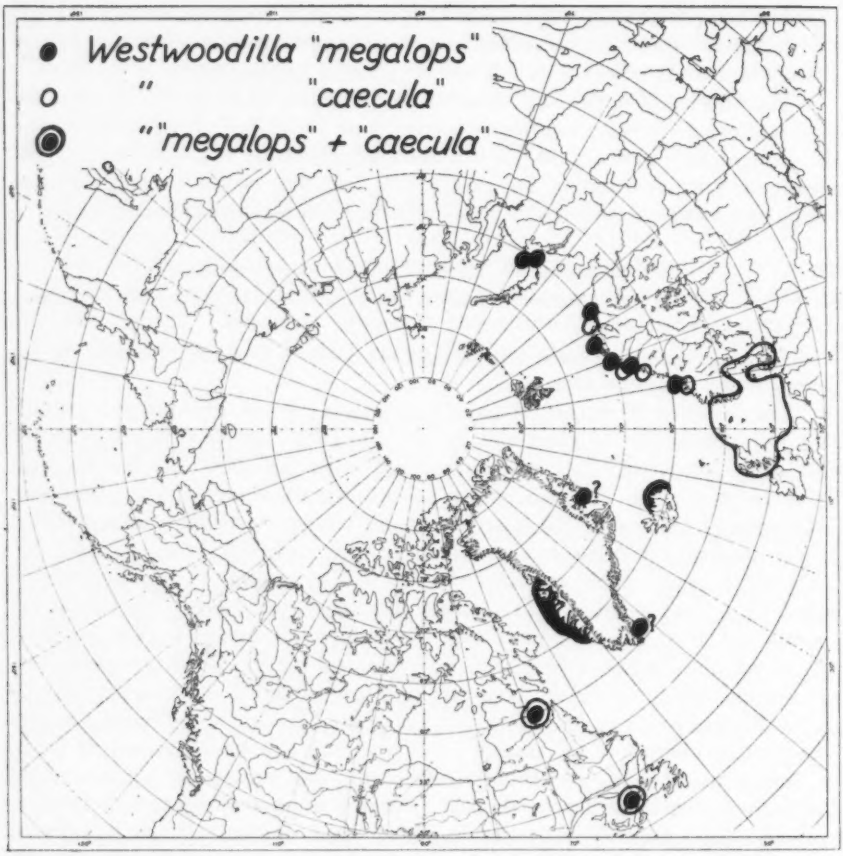

FIGURE 16. Distribution of *Westwoodilla megalops* and *W. caecula*, which are brought into synonymy in this paper (see text). Stephensen (1944a) was uncertain to which form his east Greenland specimens should be referred.

In the Ungava Bay specimens the females show the slender form described by Stephensen for *caecula*. The telson in eight of the specimens is rounded at the tip (*caecula*) but in three it is slightly emarginate (*megalops*). The antennae are short, and joint 2, per. 7, in all the specimens, is of the *megalops* shape, precisely as figured by Stephensen.

Stephensen (1944a), writing long after his 1931 paper just quoted, was unable to be certain of the indentification of specimens from east Greenland, owing to the shape of the frontal process of the head, which was intermediate between the two forms. The specimens in question have been examined by the present writer; they have the telson and joint 2, per. 7, of the *megalops* form, and since Stephensen (1931) placed specimens from west Greenland in *megalops*

on the basis of the telson, not on the shape of the head, it is possible that Stephensen himself, by 1944, was no longer certain that the species should be separated. The head shape in the Oedicerotidae is highly variable, as is abundantly shown by the studies of Enequist (1949) on material from the Skagerak. At all events the Ungava Bay specimens cannot be split into two species or even into two variants, but show characters of both the European forms. It may be that they represent the original common stock from which the two western European forms evolved.

Shoemaker (1930a) recorded both forms, referred to distinct species, from the Gulf of St. Lawrence. Examination of them shows that the population in the Gulf of St. Lawrence is similar to that in Ungava Bay. I have seen 21 specimens of the Gulf material, 15 labelled *megalops* and 6 labelled *caecula*, borrowed from the Smithsonian Institution. They were determined according to the old system of Sars (1895) and Stebbing (1906), based on the shape of the eyes and rostrum. These characters, however, as already mentioned, have since been shown to be highly variable in this family, and Stephensen (1931) reported numerous specimens which took an intermediate position in these characters. An examination of the Gulf of St. Lawrence material in the light of the distinctions proposed by Stephensen and tabulated above gives the following result:

Four specimens labelled *W. caecula* from *Prince* station 53a (see Shoemaker, 1930a):

1. Mature female. Telson slightly emarginate; per. 7 joint 2, quadrate. Body form intermediate — *?megalops*
2. Immature female. The same — *?megalops*
3. Male. Telson truncate; per. 2, joint 7, quadrate — *megalops*
4. Ovigerous female. Telson truncate; per. 7 as above; body form intermediate — *?megalops*

Two specimens labelled *W. caecula* from *Prince* station 30:

1. Male (mature?). Telson truncate but damaged; per. 7, joint 2, quadrate — *megalops*
2. Immature female. Telson rounded (*caecula*); per. 7, joint 2, quadrate (*megalops*) — mixed

Six specimens labelled *W. megalops* from *Prince* station 43:

1. Male. Telson truncate; per. 7, joint 2, quadrate, less markedly so than normal for *megalops* form — *?megalops*
2. Male. Telson missing; per. 7, joint 2, rounded — *?caecula*
3. Mature female. Telson slightly convex, not as rounded as in typical *caecula* form; per. 7, joint 2, quadrate — mixed
4. Ovigerous female. Telson truncate; per 7, joint 2, quadrate — *megalops*
5. Ovigerous female. Same as No. 4 — *megalops*
6. Mature female. Telson as in No. 3; per. 7, joint 2, quadrate — mixed

Nine specimens labelled *megalops* from *Prince* station 33:

1. Ovigerous female. Telson truncate; per. 7, joint 2, quadrate — *megalops*
2. Male. Antenna 1 longer than normal for *megalops* type; telson truncate, per. 7 quadrate — *?megalops*

3. Male. Ant. 1 as in No. 2; telson truncate; per. 7 not so markedly quadrate	?*megalops*
4. Male. Telson slightly emarginate; per. 7 quadrate	*megalops*
5. Male. Ant. 1 long; telson narrower than normal, slightly emarginate; per. 7 not markedly quadrate	?*megalops*
6. Male. Ant. 1 long (11 joints); telson as in No. 5; also per. 7	?*megalops*
7. Male. Ant. 1, 10 joints; telson long, rounded; per. 7 as in No. 5	mixed
8. Male. Ant. 1, 10 joints; telson intermediate; per. 7 as in No. 5	mixed
9. Male. Ant. 1, 9 joints; telson truncate; per. 7, joint 2, more rounded than in the above	mixed

In this material, the males were apparently mature. In all the Gulf of St. Lawrence specimens, as well as in the Ungava Bay material, side-plate 1 is more expanded than is described for *megalops* by Stephensen, approaching the condition described as typical for the *caecula* form.

The above analysis shows that the North American population of the species resembles the *megalops* form more than the *caecula* form, both of which are found in the "pure state" only in Europe, and somewhat separated in distribution there. Enequist (1949) has brought *W. caecula* and *W. acutifrons* together into one species; on the present showing, both should therefore now be included in *W. megalops*. *W. brevicalcar*, as mentioned above, lies suspiciously close to *megalops*. Further work may well show that all four forms represent a complex of variants which appear in slightly different manifestations in the various parts of the common range or in different ecological conditions.

The species, under the name *W. caecula*, has been recorded from the Japan Sea by Gurjanova (1938). The distribution of both *megalops* and *caecula* forms, as at present known, is shown in Figure 16.

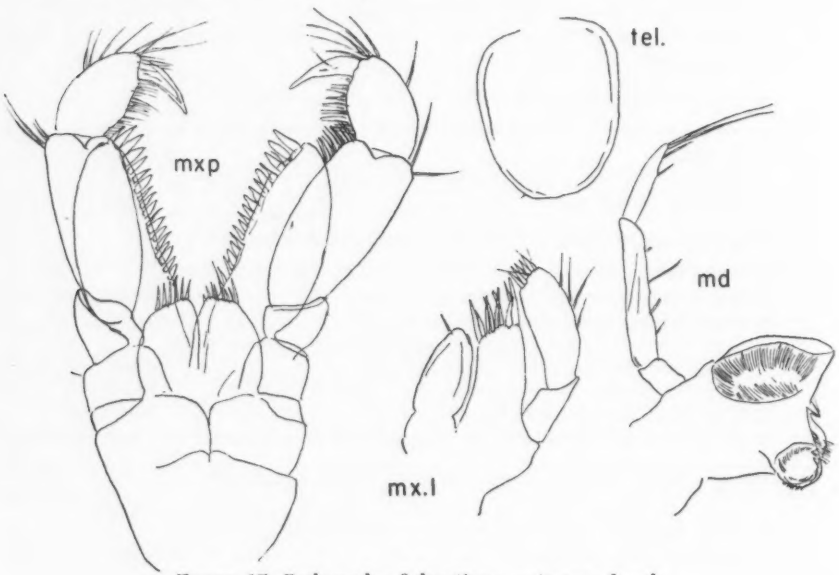

FIGURE 17. *Bathymedon ?obtusifrons*, ovigerous female.

Aceroides latipes (G. O. Sars)

One immature specimen was dredged at station 234, August 31, 1950.

The species is arctic and subarctic, circumpolar; only once before recorded from the North American arctic, from Collinson Point, Alaska (Shoemaker, 1920). Known from the East Siberian Islands, Kara Sea, Svalbard, north Norway, east and west Greenland.

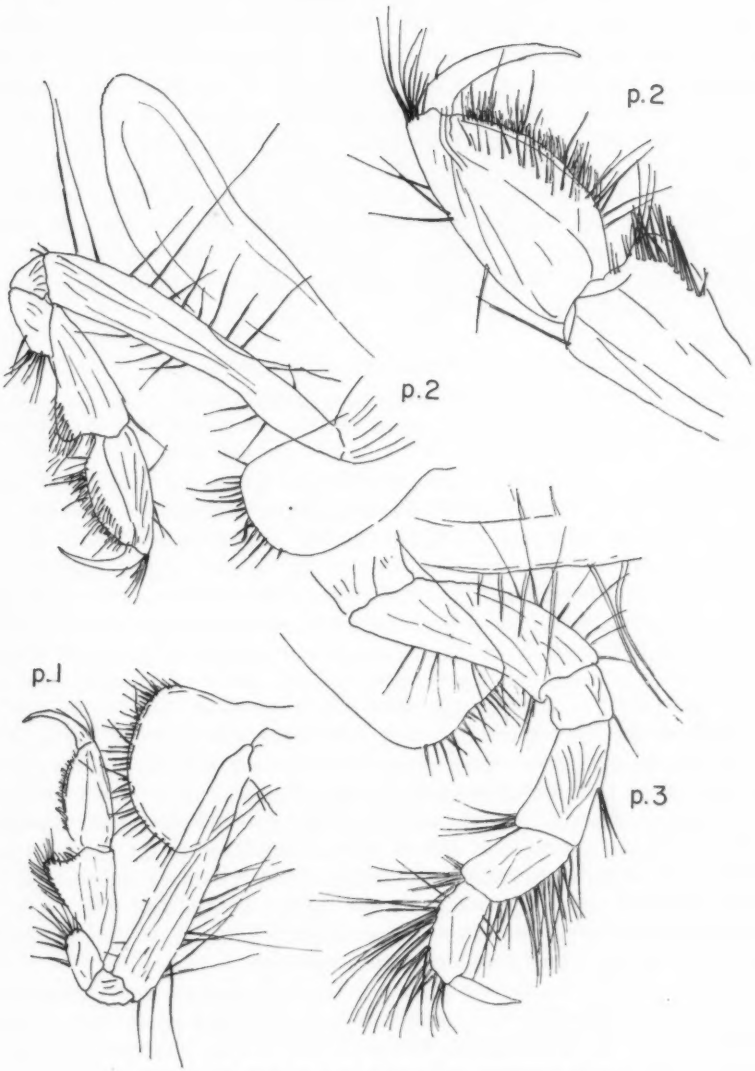

FIGURE 18. *Bathymedon ?obtusifrons*, ovigerous female.

Bathymedon ?obtusifrons (H. J. Hansen). (Fig. 17, 18)

Three specimens were caught, an immature female at station 18, July 17, 1947, and two ovigerous females, one 8 mm. long at station 102, June 30, 1949, and one 4 mm. long at station 234, August 31, 1950. The difference in size at maturity may be due to the different season of growth.

The determination has been queried because all three specimens, especially the larger of the two mature females, show differences from the original description and from Sars's (1895) figures. None of the specimens has the long spinule on the palm of per. 1 and 2. The larger female has a somewhat sharper rostrum than is normal for the species, and the telson is rather more rounded. All three specimens show a less expanded fifth joint in per. 2 (but much more expanded than in *B. longimanus* (Boeck)). These may be, probably are, local geographic variants, or they may be in part due to differences in post-maturity moults, which are well known to be complicating factors in amphipod systematics.

This species is both arctic and subarctic, being known from northeast and west Greenland, the Gulf of St. Lawrence, Franz Joseph Land and Novaya Zemlya, Iceland and north Norway. A specimen is also recorded from the Skagerak (Stephensen, 1931) and it is reported from the Japan Sea (Yashnov, 1948), and from the Kara Sea.

Monoculodes longirostris (Goës). (Fig. 19)

A mature female was dredged at station 201, June 30, 1950, and an immature specimen was taken in the plankton at station 40, August 16, 1947. The determination of the immature specimen is not certain.

The mature specimen shows deviations from the typical *longirostris* which are strikingly in the direction of *M. hanseni* Stebbing, which is known from the Kara Sea and the New Siberian Islands. In the original description of *hanseni*, Stebbing (1894) writes as follows: "The present species stands very close to *Monoculodes longirostris* Goës, but . . . the apex of the rostrum is more depressed, the second joint of the upper antennae is longer than the first instead of shorter than or equal to it, and the sides of the telson are insinuate instead of straight. The differences in the mouth-organs are very slight, but *Monoculodes longirostris* has no spines on the outer margin of the outer plates of the maxillipeds. The gnathopods of the latter species are also less widened at the palms, while in the first and second peraeopods the sixth joint is more widened distally than in the new species, and the side-plates of the third peraeopods are less wide and have the front margin straighter." In the text of the description Stebbing also described *hanseni* as having a transverse groove on the dorsal surface of the head near the base, and a slight discontinuous carina on the first three segments of the pleon, neither of which are found in the typical *longirostris*. The reader is reminded that Stebbing numbered the peraeopods posterior to the gnathopods 1 to 5 instead of 3 to 7 (see introduction of this paper).

Specimens of *M. longirostris* from east Iceland and from east Greenland in the Copenhagen collection have been compared with the Ungava Bay specimen. The latter shows the following similarities to *M. hanseni*: transverse grooves on the dorsal surface of the head; rostrum tip depressed, not so much as in Stebbing's

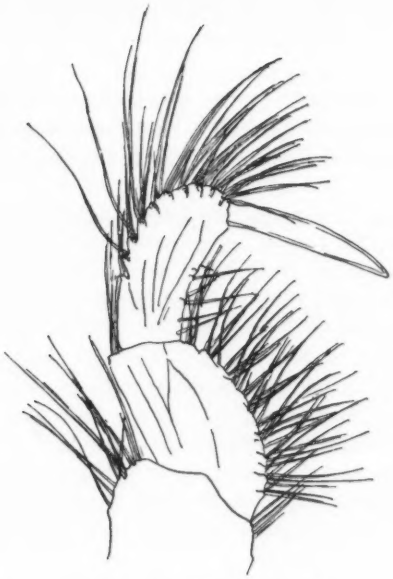

FIGURE 19. *Monoculodes longirostris,* per. 3.

description and figure of *hanseni,* but quite different from the typical *longirostris* specimens; antenna 1, joint 2 of peduncle longer than joint 1 (joint 2 is also longer in the *longirostris* specimens from Iceland and Greenland, but not to the same extent. In this character these specimens do not agree with the original description); telson, sides definitely insinuate (straight in the *longirostris* specimens); per. 1 and 2, hand slightly wider than in *longirostris,* but not significantly so; slight carina on pleon segments 1–3, more marked on the third segment than on the other two. The carina is absent from the Iceland and Greenland specimens.

In other diagnostic characters, however, the Ungava specimen agrees with the typical *longirostris,* differing from *hanseni*: no spines or hairs on the outer margins of the outer plates of the maxillipeds; antenna 1, joint 1, of peduncle a little shorter than the rostrum (longer in *hanseni*); side-plate 5, front margin straighter (in agreement with the Copenhagen collection specimens).

Joint 6, per. 3, is intermediate between the two species (Fig. 18). It is not so wide distally as in the typical *longirostris,* the pattern shown in the Iceland specimens (the Greenland examples are closer to the Ungava specimen in this character). Joint 6, per. 4, however, is similar to per. 3, and quite unlike the *hanseni* form, in which it is longer, strongly curved, and tapered to a narrow tip.

It is apparent that the Ungava Bay specimen lies between the two species; there appear also to be slight differences from the type in the Iceland and Greenland specimens, more marked in the latter. The possibility therefore arises that

we have here a good example of a geographic gradient of type between the two, and since both species are known from the Siberian coast (but in different ecological conditions (Gurjanova, 1935a)) the pattern of distribution and relation is that of the "rassenkreiss" or "artenkreiss", in which, at the two ends of the circumpolar distribution, the products of dispersal are specifically different. Such a pattern of distribution could well have occurred by means of the mechanism of dispersal from the Bering Sea region suggested by Gurjanova (1935b).

Monoculodes hanseni is at present known only from the Kara Sea and the New Siberian Islands. *M. longirostris* is known in the palaearctic as far east as longitude 117°E, to which, if the rassenkreiss pattern applies to these two species, it should have come from the west and not from the east. One specimen of *longirostris* is also recorded from Bernard Harbour in the Canadian central arctic (Shoemaker, 1920); this specimen borrowed from the National Museum of Canada, has been examined and turns out to be quite immature and therefore not referable to species with certainty. The species is also known from the Gulf of St. Lawrence (Shoemaker, 1930a) east Greenland (not west Greenland), Iceland, Svalbard, Jan Mayen, north Norway, Barents Sea and Kara Sea. It is thus an arctic and subarctic species; the lack of record from west Greenland is most probably due to the fortunes of collecting; it would be surprising if it were not there.

Monoculodes ?*krøyeri* Boeck and *Monoculodes* ?*schneideri* G. O. Sars

Immature specimens probably belonging to these two species were taken in the plankton and in the intertidal zone, but they cannot be assigned to either species with certainty.

Monoculodes latimanus (Goës)

Twenty-one specimens of this species, all immature except for one mature female, were taken in the plankton at stations 13, 22, 18 and 51. The mature female was caught on July 17, 1947.

The species is arctic and subarctic, known from Kara Strait (Stappers, 1911), Franz Joseph Land, west and north Svalbard, the Murman coast and the White Sea, north Norway, east Iceland and the Gulf of St. Lawrence, west and east Greenland. It is also recorded from the Sea of Japan (Derjavin, 1930; Yashnov, 1948).

Monoculodes edwardsi Holmes

Six specimens were taken in the plankton at station 51, in very shallow water.

M. edwardsi was described by Holmes (1905) from specimens taken on the New England coast. Shoemaker (1930a) recorded about 500 specimens from the Gulf of St. Lawrence, and it has been found also on the east coast of Hudson Bay (Shoemaker, 1926). Holmes (1905) describes joint 7, per. 5 and 6, as being over half the length of the propodus (joint 6); in the present specimens the dactyl is longer than the propodus. Otherwise they agree closely with Holmes's description and figures.

Monoculodes tuberculatus Boeck

Seven specimens, including two almost mature females, were taken planktonically at stations 13, 18, 101.

An arctic and subarctic species, recorded from the Barents Sea, Kara Sea and the New Siberian Islands, west Svalbard, north and west Norway, east and west Greenland and the Gulf of St. Lawrence. There is also a record from the Firth of Clyde, western Scotland (Norman, 1900).

Family TIRONIDAE

Syrrhoë crenulata Goës

This species was taken in the plankton at stations 13, 18 and 101, 19 specimens in all. Mature specimens were taken on July 17, 1947, and June 26, 1949. The net touched bottom at station 18.

The specimens differ from the description and figures of Sars (1895) in having only one dorsal tooth on peraeon segment 7. Specimens in the Copenhagen collection, from east Greenland, agree with the Ungava Bay material in this respect.

The species is arctic and subarctic, from Novaya Zemlya and Franz Joseph Land to the Bay of Fundy (Whiteaves, 1901); Svalbard, north and west Norway, Skagerak, Iceland, east and west Greenland, Sea of Japan.

Family CALLIOPIIDAE

Amphithopsis longicaudata Boeck. (Fig. 20)

Two ovigerous females were dredged at stations 103 and 226, on July 6, 1949, and

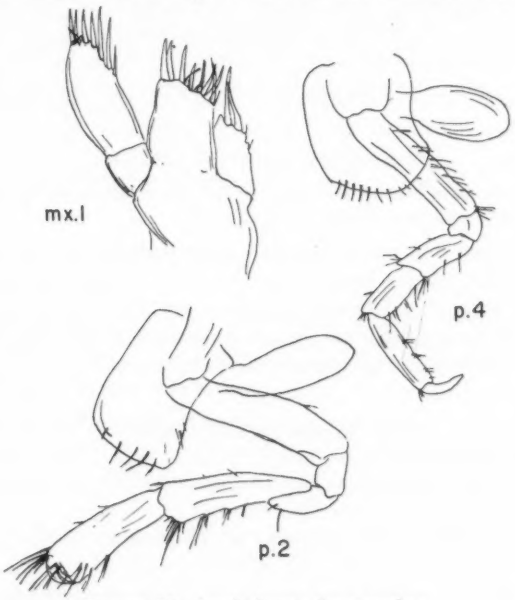

FIGURE 20. *Amphithopsis longicaudata.*

August 13, 1950. One immature female came from the stomach of a ringed seal, June 30, 1949, at Port Burwell.

These specimens differ from the descriptions of Boeck (1876) and Sars (1895) in the first maxilla, which has only two large setae on the inner plate instead of 4 (Boeck) or 7 (Sars), and in side-plate 4, in which the posterior excavation is very slight. They are not important differences, and in the case of side-plate 4 the specimens in the Copenhagen Museum collection show considerable variation; there is in fact a difference in the extent of excavation even between the two mature Ungava Bay specimens. The individual with the lesser excavation is shown in Figure 20.

The species has been recorded from the subarctic only: White Sea, north and west Norway, Iceland, west Greenland, Gulf of St. Lawrence and Hudson Bay.

Halirages mixtus Stephensen

Seven specimens, six immature and one maturing female, were taken in the plankton at station 40, August 16, 1947.

The species was established by Stephensen (1931) on specimens from Ingolf's Fjord, east Greenland, latitude 66°15'N. The present record from Ungava Bay is the first outside the type locality. The maturing female differs from Stephensen's description only in the telson, which has a single notch at the tip instead of a triple notch (the two outer notches are missing). The immature specimens have the telson as described by Stephensen. The telson in the genera *Halirages* and *Apherusa* is inclined to be highly variable. Apart from the telson, the agreement with *mixtus* is complete, including the diagnostic characters given by Stephensen, namely the process on joint 3, antenna 1, the quadrangular subantennal corner of the head and the broad second joint in per. 5–7. The eyes, which were damaged in Stephensen's type specimen, are round and black.

Halirages fulvocinctus (M. Sars)

One female, not quite mature, was taken in the dredge at station 33. Six specimens were taken in cod stomachs (*Gadus callarias*) at Port Burwell.

This species is arctic and subarctic, present also in the Skagerak. Kara Sea, Barents Sea, Franz Joseph Land, New Siberian Islands and "far eastern seas" (Yashnov, 1948), coast of Norway, Svalbard, Jan Mayen, Iceland, east and west Greenland, northeast Ellesmere Island, southeast Baffin Island, Gulf of St. Lawrence, Hudson Bay and the coast of Nova Scotia.

Halirages megalops (Bucholtz)

Syn.: *Paramphitoë megalops* Bucholtz, 1874.
Apherusa megalops Shoemaker, 1930a; Dunbar, 1942.
Halirages megalops Stephensen, 1931, 1944a.

This species was taken in the plankton only, 70 specimens in all, at stations 7, 9, 33, 51, 101, 123 and 225.

There seems to be no good reason to keep the genera *Halirages* and

Apherusa separate. As Stephensen (1931) has pointed out, it has been necessary to modify the descriptions of both to such an extent that there remains only one small difference between the two—the presence of calceoli on the antennae in *Halirages* and their absence in *Apherusa*, and in some cases, as in the present species, the calceoli are few.

This species is common where found, but it has been recorded so far only from east and west Greenland, the Barents Sea (Yashnov, 1948), various stations in the Canadian eastern arctic (Dunbar, 1942), the Gulf of St. Lawrence (Shoemaker, 1930a) and Bernard Harbour in the central arctic (Shoemaker, 1920). Stephensen (1944a) calls it a "low-arctic" (subarctic) species. The records from northeast Greenland and the Canadian central arctic cannot be called subarctic on the criteria used here, but these records are all from shallow water, probably above the thermocline, and therefore from water which is heated in summer by insolation. If, therefore, the limiting distributional factor is the temperature during the breeding period, it may be that this species is to be looked upon as a subarctic form which has invaded shallow water farther north, or as a relict of a warmer part of the climatic cycle. This pattern may also fit other species. Stephensen uses the term "low-arctic" to include such shallow water areas in regions otherwise purely arctic, following Hofsten (1915), Lemche (1941), etc. (see below, discussion).

In Ungava Bay, ovigerous females were taken on July 3, July 7, July 11 and August 10, 1947, and June 26 and August 10, 1949.

Apherusa glacialis (H. J. Hansen)

Seventy-three specimens of this common pelagic species were taken in the plankton, at stations 1, 7, 9, 13, 18, 41, 56, 103, 203 and 303. There were no ovigerous females in the material.

This is a circumpolar species, arctic and to a lesser extent subarctic, pelagic, usually in the upper layers. Known from the Arctic Sea in the north to the tip of south Greenland, and from Jones Sound to the Gulf of St. Lawrence. Hudson Strait, north coast of Alaska and Bernard Harbour, N.W.T.; Kara and Laptev Seas, and Svalbard.

Calliopius laeviusculus (Krøyer)

Syn.: *Calliopius rathkei* (Zadd.)

Eighty-seven specimens, all immature, were taken, all but one in plankton nets. The single specimen caught on the bottom was found on a seal skull left in seven fathoms overnight at station 125A. The others were taken at stations 31, 40. 43, 51, 125, 129 and 304. All these are shallow water stations close to shore.

C. laeviusculus and *C. rathkei* were brought together to a single species by Stephensen (1931), who showed that the small distinguishing features were found in all degrees of intergradation. Both forms occur in the Ungava Bay material.

The species is arctic, subarctic and boreal, predominantly subarctic. It does not appear to have been recorded yet from the Siberian coast east of the Barents Sea, but it is known from the north Pacific including the Japan Sea; the

Canadian central arctic and eastern arctic, west Greenland, Iceland, Faeroes, the British Isles, the North Sea and the Baltic, the coast of Norway east to the White Sea, west Svalbard and Franz Joseph Land.

Family PLEUSTIDAE

Pleustes panoplus (Krøyer)

Seven specimens were taken. Two immature individuals were caught in plankton nets at stations 18 and AS-28 (Acadia Cove, Resolution Island); two females approaching maturity were dredged at stations 11 and 216; and three specimens were taken from the stomach of a bearded seal off the mouth of the Whale River.

A circumpolar arctic and subarctic species, recorded from the New England coast to Ungava Bay (Smith, 1884) and Baffin Bay and eastwards over Greenland, Svalbard, Franz Joseph Land to the New Siberian Islands and the Japan Sea, south in northwest Europe to Bohuslän.

Pleustes medius (Goës). (Fig. 21)

Five specimens were dredged at station 102.

Brüggen (1909) considered that this species, together with others, was a variation or immature stage of *P. panoplus*. This has not been followed by later authors, and indeed the evidence upon which Brüggen based his opinion was

FIGURE 21. *Pleustes medius*, mandible.

very slight. *Pleustes medius* differs widely from *panoplus* in size at maturity, lack of body ridges, strong molar in the mandible, characteristic side-plates 1 and 2, different form of per. 1 and 2 and of pleon 3; side-plate 4 is also entirely different. Even allowing for the pitfalls of amphipod systematics the two cannot be put together.

Since the original description of Goës, the species has been redescribed by Stephensen (1938) and Shoemaker (1930a), the latter with new figures. Neither author mentions the fact that the mandibular molar is strongly developed, in

contrast to *panoplus* and also in disagreement with the generic description of Stebbing (1906) and others. The mouthparts have in fact never been described. The strong molar, which requires a restatement of the generic description, is illustrated in Figure 21, and the character has been confirmed by the examination and dissection of specimens (co-types) in the Copenhagen Museum collection, in which the mandibular molar is equally stout, the left with a larger triturating surface than the right.

This species has not often been recorded. It is known from west and northwest Svalbard, the White Sea and the Murman coast, the Kara Sea (Gurjanova, 1935a), and the Gulf of St. Lawrence (Shoemaker, 1930a).

Parapleustes pulchellus (Krøyer)

Syn.: *Neopleustes pulchellus* Stebbing, 1906; Shoemaker, 1930a.
Parapleustes pulchellus Stephensen, 1938, 1944a, 1944b.

Five immature specimens of this species were taken in the benthos at stations 103 and 226.

This species is recorded from the subarctic belt and to a lesser extent from arctic areas, from the Maine coast to Davis Strait, Iceland, Svalbard and Franz Joseph Land, the Barents and White Seas, north and west Norway and the deep water of the Norwegian Sea; New Siberian Islands. It is not known from east Greenland.

Parapleustes boecki (H. J. Hansen)

Syn.: *Neopleustes boecki* Stebbing, 1906.

Four specimens were dredged at stations 58, 208 and 226. Two of them were mature females, taken on July 28, 1948, and July 20, 1950.

Della Valle (1893) put this species together with *P. pulchellus* and other species of the genus, but this has not been followed by others, nor is it at all reasonable; the species does not agree with Della Valle's own description and it is easily and immediately separable from *P. pulchellus*.

P. boecki has been reported hitherto only from west Greenland, from Disko Bay southwards (Hansen, 1887), and from the New Siberian Islands (Yashnov, 1948).

Parapleustes bicuspis (Krøyer)

Syn.: *Neopleustes bicuspis* Stebbing, 1906.

Six immature specimens were taken in the plankton at station 123.

According to Stephensen (1917) this is one of the commonest amphipods on the southwest Greenland coast. In Canada, it has already been recorded from Ellesmere Island (Sars, 1909), Baffin Bay (Ohlin, 1895), Labrador (Packard, 1867) and Hudson Bay (Shoemaker, 1926). It is a species of wide distribution in the Atlantic boreal, subarctic and arctic, and it is known from the Barents Sea, Franz Joseph Land, White and Kara Seas (Yashnov, 1948); east and west Greenland, Iceland, Svalbard, Norway, Skagerak and Øresund (Dahl, 1946b), northwest France.

Parapleustes assimilis (G. O. Sars). (Fig. 22)

Syn.: *Neopleustes assimilis* Stebbing, 1906.

Twelve specimens were taken in the benthos at stations 18, 103 and 226. Ovigerous females were found on July 6, 1949, and August 13, 1950.

The specimens differ from Sars's description and figures in two characters: in per. 2 the hind margin of joint 6 is more rounded, with the palm poorly defined. The tooth on the palm is present, but a little larger. The finger is slightly longer (Fig. 22). In these variations from the type the Ungava Bay specimens are in agreement with specimens in the Copenhagen collection from southwest Greenland (Bredefjord).

FIGURE 22. *Parapleustes assimilis*, per. 2.

Predominantly a subarctic species, but found also in the boreal (off Liverpool, near Helgoland, Firth of Forth and Shetlands Islands), and in the arctic (Scoresby Sound, New Siberian Islands). West Greenland, Hudson Bay, Faeroe Islands, Skagerak (Enequist, 1949), Barents and White Seas. It is a shallow water species, and as regards the records from Hudson Bay, Scoresby Sound and the New Siberian Islands, the same considerations may apply here as in the case of *Halirages megalops* (above).

Parapleustes sinuipalma n. sp. (Fig. 23, 24)

One ovigerous female was dredged at station 11, July 12, 1947. An immature male which may belong to the same species (see below) was taken in the plankton at station 33, August 10, 1947.

Body not carinate, without dorsal teeth in the female, but with pleon segments 1 and 2 dorsally bluntly produced. Head as long as the first two thoracic segments, lateral angles produced, rounded, lower angles sharp. Side-plate 1 very little expanded distally, side-plates 1, 2 and 3 with minute notch and tooth at lower hind corner. Pleon segment 3, postero-lateral corner produced into a small tooth. Eyes large, almost round. Antenna 1, first joint of peduncle as long as second and third combined, flagellum long, over half body length. Mouthparts typical of the genus. Left mandible with accessory plate, maxilla 1 with 2 setae on inner plate. Maxillipeds, third joint of palp not distally attenuated beyond the finger (this agrees with other species of the same genus established since Stebbing, 1906 (Holmes, 1908; Gurjanova, 1938), and the generic description should be altered accordingly). Per. 1 and 2 alike, hand (joint 6) rather long, slightly larger in per. 2 than in per. 1, palm slightly sinuous and richly armed with spinules; finger long. Telson oval, more or less smoothly rounded

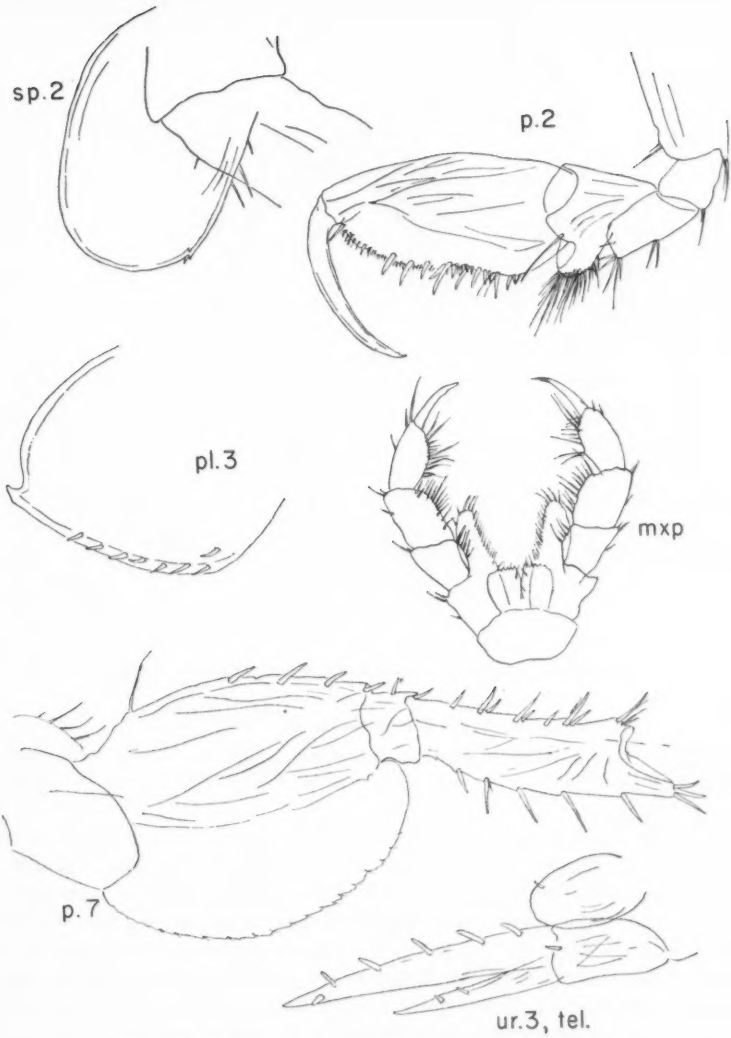

FIGURE 23. *Parapleustes sinuipalma* n. sp., ovigerous female.

at the tip and (in the type specimen) asymmetrically armed with one small spinule. Length 12.5 mm.

An immature male specimen taken in the plankton at station 33 agrees with this description in every detail except that there are three dorsal teeth. It is possible that this is the male of the species, but the matter is uncertain. The type specimen (No. MJD–002) is in the collection of the Redpath Museum, McGill University.

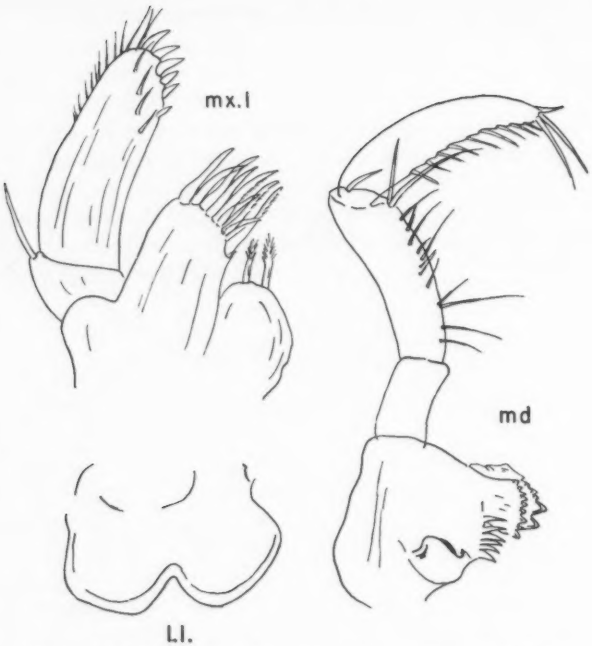

FIGURE 24. *Parapleustes sinuipalma* n. sp., ovigerous female.

Parapleustes glabricauda n. sp. (Fig. 25, 26)

Six specimens, including an adult male and two ovigerous females, were dredged at station 208, July 20, 1950; one male was taken at station 103, also in the benthos, on August 7, 1949.

Small but robust, back broadly vaulted, smooth. Side-plate 1 expanded below, rounded. Rostrum short, blunt; head a little shorter than first two body segments, lateral angles broadly rounded, lower angles recessive. Side-plates 1–3 without denticle, side-plate 4 only slightly deeper than broad. Pleon 3 quadrate, corner rounded. Eyes not large in the female, reniform, large in the male. Antenna 1, joint 1 of peduncle almost as long as the next two joints together, flagellum a little over half the body length. Antenna 2 shorter, fourth and fifth joints of peduncle of equal length, peduncle reaching beyond the peduncle of the first antenna. Upper lip asymmetrically bilobed. Mandibular palp sturdy, molar fairly prominent, but without triturating surface, much weaker than in the genera *Stenopleustes* or *Sympleustes*. Maxilla 1, inner plate with only one seta. Maxillipeds, outer plate very small, third joint of palp produced beyond the insertion of the finger; finger strong. Per. 1, fifth joint a little longer than sixth, sixth at least twice as long as broad, hind margin richly supplied with long setae, 4 to 5 small spinules at angle of palm. Per. 2, joint 6, broad, fore and hind margins almost parallel, palm well defined, more uneven in outline in the male

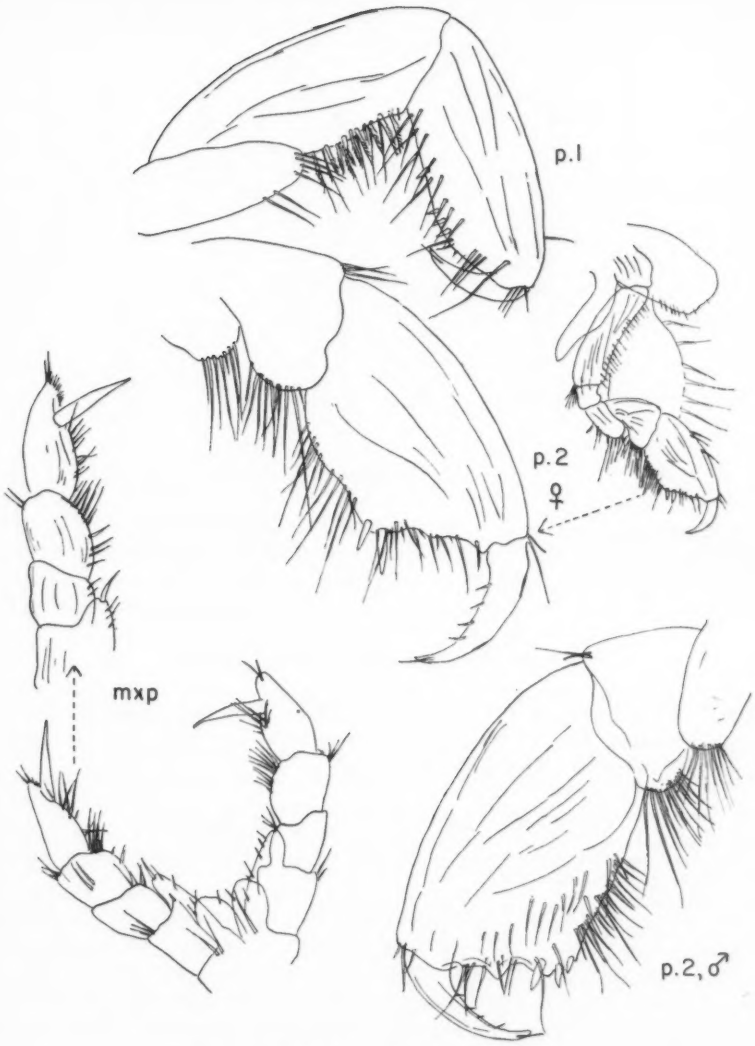

FIGURE 25. *Parapleustes glabricauda* n. sp.

than in the female. Per. 3–7 moderately sturdy. Uropods glabrous in appearance, poorly armed with small spinules, uropod 3 with only 1–2 setae on each ramus; the outer ramus a little over two-thirds of the inner length. Telson oval, small terminating in a rounded point, armed with two small setae. Length (female) 4–5 mm., male a little larger. The species is distinguished from others of the genus by the small outer plates of the maxillipeds, the shape of per. 1 and 2, and

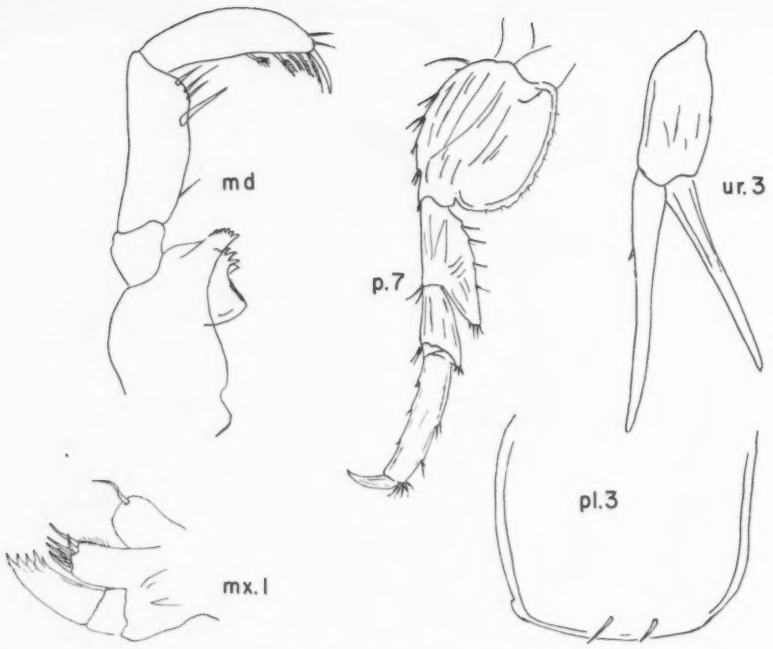

FIGURE 26. *Parapleustes glabricauda* n. sp.

the poorly armed uropods. The type (No. MJD–003) and co-types are at the Redpath Museum, McGill University; one co-type has been deposited in the Zoological Museum of Copenhagen University.

Sympleustes olriki (H. J. Hansen). (Fig. 27)

One female and one immature specimen were taken at stations 13 and 18, in both cases in stramin nets which touched bottom.

Like *Parapleustes boecki*, this species was found and described originally by Hansen (1887) from west Greenland (Prøven), and has been recorded since only from the northern Russian coast (Kara Sea, Yashnov, 1948). Also like *P. boecki* it was lumped together with another species (in this case *S. latipes* M. Sars) by Della Valle (1893), and immediately separated again by later authors, including Stebbing (1906). The reasons for Della Valle's fusion of the two species are obscure, and are in fact not expressed at all. The deep incision, or bight, on the palm of per. 2 (Fig. 27) is an adult character in both species, but the form of the incision and of the whole hand is quite different in the two. Moreover in his description of *S. latipes*, Hansen (1887) specifically stated that in younger specimens the incision is much less, as in other instances of the same sort in the amphipods (for instance in *Metopa norvegica* above), and it is therefore very unlikely that *S. olriki* can be looked upon as a sub-adult stage of

FIGURE 27. *Sympleustes olriki*, per. 2.

latipes, as Della Valle suggested. There are other clear differences between the two species, for example the total absence of a dorsal keel in the present species.

This species has been taken only in west Greenland, the type locality, in the Kara Sea (Yashnov, 1948) and now in Ungava Bay.

Sympleustes ***buttoni*** n. sp. (Fig. 28, 29)

Four mature females of this species were taken in the benthos at stations 40 (August 10, 1947) and 226 (August 13, 1950).

Body fairly slender, back smooth. Side-plates typical of the genus in general shape and size, rounded below, numbers 1–3 with a minute notch and tooth, armed with a spinule, at lower hind corner. Pleon 3, postero-lateral corner produced into a very small tooth. Eyes subcircular, large. Head a little longer than the first two body segments, rostrum small, blunt, lateral corners produced but rounded, lower corners prominent and sharp. Antenna 1, peduncle joints 2 and 3 together a little shorter than joint 1, flagellum reaching about half length of body. Antenna 2 shorter, peduncle joints 4 and 5 equal. Mouthparts typical of the genus, but inner plate of maxilla 1 has only one seta, not two. Mandible, molar strong, cylindric. Per. 2, hand (joint 6) as long as head, per. 1 only slightly shorter, of similar shape. Palm smooth, convex, with one small tooth in the middle, defined by a heavier armament of spinules in per. 2 than in per. 1. Per. 3–7 rather slender. Uropods, third the longest, all three pairs well armed with short strong spinules. Telson oval, margin rounded, armed with two very small short setae. Length (female) 9 mm.

This species is fairly close to *S. glaber* (Boeck), but after close comparison of these specimens with *S. glaber* from southeast Greenland and from southeastern Canada (St. Andrews, N.B.), it is clear that both they and those described in the next species do not belong to *glaber*, unless that species is a

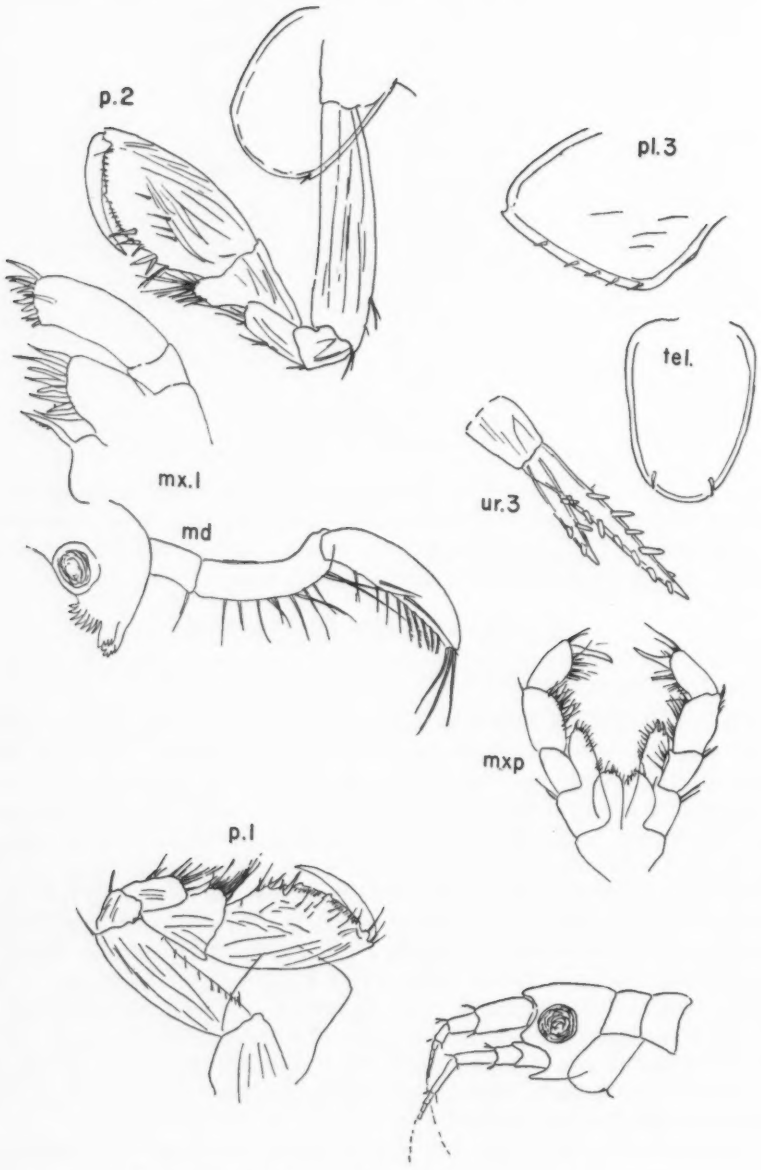

FIGURE 28. *Sympleustes buttoni* n. sp., ovigerous female.

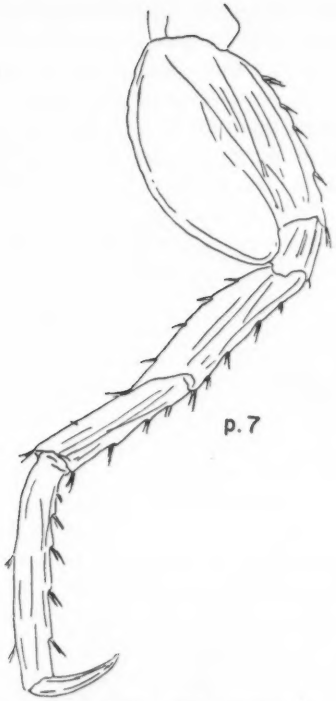

FIGURE 29. *Sympleustes buttoni* n. sp.

great deal more variable than our present knowledge of it indicates, and much more variable than other species of the family Pleustidae. *S. buttoni* differs from *glaber* in a variety of characters: There is no process on the first joint of the peduncle of antenna 1; the lateral angles of the head are more rounded; there is only one seta on the inner plate of the first maxilla (in this the species differs from the generic description in Stebbing (1906), as do two of the three new species of the genus described by Gurjanova (1938) and one by Chevreux (1927)); the notch and tooth on side-plates 1–3 are much smaller; in per. 7 the expansion of the second joint is smaller and of a different shape; and the relative length of the uropods is not the same. The type specimen (No. MJD–004) and one co-type are at the Redpath Museum, McGill University, and two co-types have been deposited in the Zoological Museum, Copenhagen.

Sympleustes glabroides n. sp. (Fig. 30)

Four ovigerous females and five immature specimens were dredged at station 226, August 13, 1950. One immature specimen was dredged at station 103, and one small immature individual, possibly belonging to the same species, was taken in the plankton at station 40.

Body fairly robust, back smooth and broadly vaulted. Head small, about as

long as the first two body segments. Rostrum small and blunt, lateral angles of head produced and acute, lower angles acute, forming large sinus. Eyes large, almost round or with hint of kidney-shaped anterior margin. Side-plate 1 small; side-plates 2–4 very deep, rounded, angular below. Side-plates 1–3 with very strongly developed hooked tooth on lower hind angles. Pleon 3 produced with rounded tip, without tooth. Antenna 1, first joint of peduncle longer than second and third together, produced medio-ventrally into a sharp point more than half

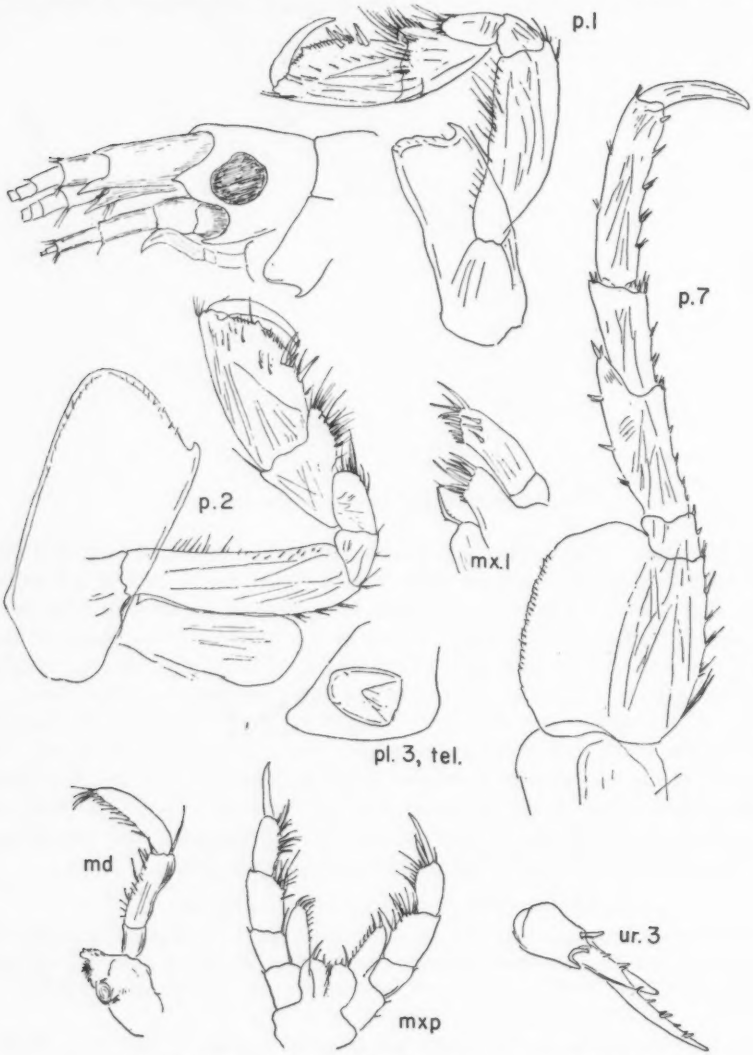

FIGURE 30. *Sympleustes glabroides* n. sp., ovigerous female.

as long as joint 2. Flagellum broken in present specimens, probably a little over half body length. Antenna 2 shorter, joint 5 of peduncle somewhat shorter than joint 4. Mouthparts typical of the genus, but maxilla 1 with only one seta on inner plate. Maxillipeds, finger of palp strong. Per. 1 and 2 similar in shape, per. 2 the larger, hand almost as long as head. Palm smooth except for one tooth, fringed with setae (similar to *S. buttoni*), palm defined by strong spines. Per. 3–7 fairly robust. Uropods, second pair the longest, all armed with spinules. Telson rounded, with two small setae on dorsal surface near the tip. Length 7.5 mm. The type (No. MJD–005) and co-types are lodged at the Redpath Museum, McGill University; two co-type specimens are in the collection of the Zoological Museum, Copenhagen.

In going through Dr. K. Stephensen's collection of Pleustids in the Copenhagen Museum, I found a vial containing six specimens marked "?*S. pulchellus*?" and "all?", from Tasiusak, east Greenland, 22/10/98, taken by the Amdrup Expedition in 6 to 10 metres, stony bottom with algae. These turned out to belong to the present new species. The explanation may be that the specimens of *pulchellus* were removed from the vial after Stephensen's label was written, and the information not corrected. At all events, there are very great differences between *pulchellus* and *glabroides*.

Like *S. buttoni*, this species has points in common with *S. glaber*, although different points. *S. glabroides* and *S. glaber* agree in having rather strong teeth on side-plates 1–3, and in the produced point on the first joint of the peduncle of antenna 1. Both these characters, however, are much more pronounced in *glabroides*, and the present species is further separated from *glaber* in the setation of the inner plates of the first maxillae, in the shape of pleon 3, and in the relative length of the uropods.

The new species is also fairly close to *S. uncigera* Gurjanova (1938), resembling it in the strong teeth on side-plates 1–3 and in the shape of per. 1 and 2. It differs from *uncigera* in pleon 3, in the shape of the uropod rami (short and broad in *uncigera*), and in the eyes, which are smaller in *uncigera*. Specimens of *uncigera* in the Copenhagen collection, incidentally, show sharp lower angles in the head, not recessive as figured by Gurjanova (1938).

In present systematic practice, there is no doubt that these two last-described forms must be established as new species. The possibility that they (and also *S. uncigera* Gurjanova) represent extreme variations of *S. glaber* is remote but not out of the question; the matter could only be settled by breeding experiments or perhaps by much more intensive collecting over the whole range.

The family Pleustidae is in need of revision, especially as regards the generic descriptions. In *Pleustes* the molar of the mandible may be strong or weak; in *Parapleustes* (*Neopleustes*) the third joint of the palp of the maxilliped is not always produced beyond the articulation of the fourth joint, and there may be one or two setae on the inner plates of the first maxillae; in *Sympleustes* there may be the same inter-specific variation in the setation of the inner plates of the first maxillae. It appears that the only character that separates the genera *Parapleustes*, *Stenopleustes* and *Sympleustes* is the structure of the mandibular molar.

Family PARAMPHITHOIDAE

Paramphithoe hystrix (J. C. Ross)

Fourteen specimens, including seven females and four males approaching maturity, were dredged at station 203, July 8, 1950; one mature male was taken at station 221, August 3, 1950. One specimen came from the stomach of a bearded seal 15 miles ENE of the Gyrfalcon Islands.

The species is arctic and subarctic, probably circumpolar, not yet reported from the Canadian central arctic nor from Alaskan waters, but known from Jones Sound and Ellesmere Island (Sars, 1909), the Gulf of St. Lawrence, Newfoundland and the Bay of Fundy, west and east Greenland, Iceland, Svalbard, Norway south to the Skagerak, Barents and Kara Seas, Franz Joseph Land and the eastern Siberian shelf (Runnstrøm, 1928).

Family ATYLIDAE

Atylus carinatus (J. C. Fabr.)

Eight specimens were taken, one male at station 51, in very shallow water in a plankton net; three immature specimens from the stomach of an eider duck at Port Burwell, three from the stomach of a bearded seal at the mouth of the Koksoak River, and one from a ringed seal at the Button Islands.

This is a circumpolar arctic and subarctic species, of similar distribution to the last species, *Paramphithoe hystrix*. It has already been recorded from several localities in the Canadian arctic (Oldevig, 1917; Shoemaker, 1920, 1926; Stephensen, 1944a). It has not been recorded from the Gulf of St. Lawrence, nor does it extend so far down the Norwegian coast as *P. hystrix*. It is reported from the Sea of Okhotsk (Derjavin, 1930).

Family EUSIRIDAE

Eusirus cuspidatus Krøyer

Seven specimens were obtained, all immature, five in the benthos at stations 18, 33, 103 and 231; one in the plankton at station 101, and one from a cod stomach at Port Burwell.

E. cuspidatus is an arctic and subarctic species, known in North America from Jones Sound, Newfoundland (Frost, 1936) and the Bay of Fundy; west and east Greenland, Iceland, Svalbard, etc., south to Tromsø in Norway, east to the New Siberian Islands. Probably circumpolar.

Rachotropis aculeata (Lepechin)

Sixty-seven specimens were taken, eleven of them at stations 18, 102, 107 and 203. Mature females were caught on June 30 and July 7, 1949, and July 8, 1950. The remainder were taken from bearded seal stomachs at Burwell, the mouth of the Koksoak River, the Gyrfalcon Islands and at station 202.

Juvenile specimens in the material show the following differences from the adults: the hind margin of peraeon segment 7 has five blunt projections, which develop in the adult into three sharp dorsal points and two sharp hind corners; the point on joint 2, per. 7, is present but not sharp; joint 2, per. 5 and 6, has a

backward expansion, not found in any other species of the genus, which develops into the distinctive sharp point of the adult.

This is again an arctic and subarctic species of wide, probably circumpolar distribution recorded from the Gulf of St. Lawrence and from an uncertain station in the Hudson Strait or Labrador area (Shoemaker, 1920, 1930a). For details of distribution see Stephensen (1940a), Stappers (1911) and Oldevig (1917). It is known from the Japan Sea and the Laptev and Kara Seas (Gurjanova, 1938, 1935a; Yashnov, 1948).

Rachotropis inflata (G. O. Sars)

Thirteen specimens of this species were taken, probably in the benthos, on two occasions when the stramin net touched bottom, at stations 13 and 18. Females and males approaching maturity were caught at the latter station on July 17, 1947.

This is a subarctic species, according to present knowledge, extending also into the arctic regions in northeast Greenland. It is known from the Gulf of St. Lawrence, west and east Greenland, west and north Norway, Svalbard, the Skagerak, the Kara Sea and the Sea of Japan.

Family PONTOGENEIDAE

Pontogeneia inermis (Krøyer)

This is a very abundant species in Ungava Bay. Altogether 267 specimens were taken, all but two in the plankton, at stations 1, 7, 9, 33, 38, 40, 37, 51, 101, 123, 124 and 228. These are all quite shallow water stations, all under 30 metres and most of them much less (see stations list–Dunbar and Grainger, 1952). The single specimen taken in the dredge was found at station 3. Ovigerous females were caught on July 3, August 10, June 29 and August 29, 1947; and June 26, August 10, 1949. One specimen was taken from the stomach of a ringed seal at the mouth of the Koksoak River, July 1, 1948, an ovigerous female.

This is probably a Pacific subarctic species which has spread from the Bering Sea eastwards as far as east Greenland but not to Iceland, Svalbard or Norway; and westward only to the eastern Siberian shelf. There is a gap in its distribution between east Greenland and eastern Siberia. It is recorded from the New England coast, Newfoundland and the Gulf of St. Lawrence, Gabriel Strait (Hudson Strait), Labrador, Hudson Bay, Bernard Harbour, west and east Greenland, the Japan Sea and the Bering Sea. For details see Stephensen (1944a). A former record from the coast of Norway has been found to be incorrect (Stephensen, 1940a).

Family GAMMARIDAE

Weyprechtia pinguis (Krøyer)

Nine specimens of this species were taken, of which only one, an apparently mature male, was dredged from the benthos, at station 45 (August 23, 1947). Seven were immature specimens except for one maturing female, and were all taken in plankton nets at stations 123 and 128. One immature individual came from the stomach of a ringed seal at Port Burwell.

There is a sex difference in this species which is not mentioned in the literature. Per. 1 and 2, joint 6, is somewhat heavier in the female than in the male, and the palm is a little less oblique. Specimens from east Greenland

(Denmark Strait at Hvalrosnaes) in the Copenhagen collection showed the same differences between the sexes.

This is a circumpolar species, arctic and subarctic, already recorded from several localities in arctic and subarctic Canada: Ellesmere Island, west Baffin Bay and Davis Strait, Bernard Harbour and Hudson Bay. Greenland, Svalbard, Barents Sea, Kara Sea and Laptev Sea, eastern Siberia and the Pacific subarctic.

Gammarellus homari (J. C. Fabr.)

Twenty specimens were taken. Most of them are small, taken in the plankton at stations 1, 3, 7, 103, 124, and at Acadia Cove, Resolution Island. A large female, not mature, was dredged at station 3. One was taken in a ringed seal stomach, station 210A, and two from cod stomachs at Port Burwell.

In the large female the last epimer (pleon 3) was more rounded than in the adult Norwegian specimen figured by Sars (1895) and the telson showed two notches instead of one, with a small spine in each notch. Specimens from Iceland in the Copenhagen collection also had two notches, without spines. These specimens were mature.

This is a shallow water form of wide distribution in the boreal, subarctic and arctic zones, known from the Canadian eastern arctic (Ellesmere Island, Jones Sound) south to the Bay of Fundy; Greenland, Iceland, Svalbard, Franz Joseph Land and Novaya Zemlya, the White Sea and the Murman coast, and along the Norwegian coast to the southern Baltic, the British Isles and western France. It does not appear to have been recorded from east of Novaya Zemlya nor from the Pacific region.

Melita dentata (Krøyer)

One large but immature specimen of this species was taken in the dredge at station 126, August 23, 1949.

An exceedingly widely distributed species, taken in all depths down to 300 metres in the boreal, subarctic and arctic zones from the Gulf of Mexico to the arctic archipelago, and from the British Isles to Svalbard and the Kara Sea; both coasts of Greenland. It is also known from the Pacific (Kamchatka, Japan Sea, Puget Sound). For details of localities and references see Stephensen (1940a) and Oldevig (1917).

Gammarus spp.

The systematics of the species of *Gammarus* have undergone revision in the past few years owing to (1) the final recognition of *Gammarus zaddachi* Sexton, which was first described many years ago (Sexton, 1912) but which was stubbornly overlooked by zoologists (including the writer) until recently; (2) the subdivision of *G. zaddachi* into three subspecies (*G. zaddachi zaddachi* Spooner, 1947; *G. z. salinus* Spooner, 1947; and *G. z. oceanicus* Segerstråle, 1947); (3) the establishment of *Gammarus setosus* by Dementieva (1931) as a species separate from *Gammarus locusta* (L). (*setosus* was described fully for the first time by Stephensen (1940a) as a subspecies of *locusta*, but Segerstråle (1947) demonstrated that it is as different from *locusta* as is

zaddachi); and (4) the final establishment of *Gammarus wilkitzkii* Birula as a separate species by Gurjanova (1930) and Segerstråle (1947) (but not by Stephensen and others (see below)).

All of these species were confused with *G. locusta* in the past, and consequently all former records of *locusta*, before 1947, especially in northern regions, become suspect. According to Segerstråle (1947) the most northerly records of the true *locusta* are from northeast Iceland and north Norway, latitude 70.5°N. It is probably absent from Greenland (see below) and also from North America. All records of *locusta* from North America, so far examined, have turned out to refer to *zaddachi*, to the subspecies *oceanicus* (Spooner, 1951; Segerstråle, private communication). *Gammarus locusta* is not present in the *Calanus* expeditions' material from Ungava Bay, nor in any of the McGill University collections from Baffin Island.

Gammarus zaddachi Sexton, subsp. *oceanicus* Segerstråle 1947. (Fig. 31)

This is exceedingly abundant in Ungava Bay, and was taken by hand in the intertidal zone and also in plankton nets over shallow bottoms. It was not taken in the dredges or trawls. In the intertidal zone it was collected in large numbers at stations 1A, 5, 8, 64, 107B, 112, 205, 212, 217, 229 and 235, and generally in the estuary of the Koksoak River at low water. Planktonically it was obtained at stations 31, 40, 37, 51, 201C. Ovigerous females were taken on June 24, 1947, July 11, 1949, and July 30, 1950. A few specimens were taken in cod stomachs at station 224, Port Burwell (this was the only fishing station at which cod stomachs were found to contain either *G. zaddachi or setosus*). Seven specimens were taken from ringed seal stomachs.

Spooner (1947), in establishing the subspecies *G. z. salinus* and *G. z. zaddachi*, showed that the two subspecies could not produce fertile eggs on crossing. No such breeding experiments have so far been done on the subspecies *salinus* and *oceanicus*, and indeed the two are very close together morphologically, as is admitted by Segerstråle (1947). *G. z. salinus* is a brackish water form, so far reported only from northwestern Europe, whereas *oceanicus* is found mainly in fully marine localities; where the two overlap they are sometimes difficult to distinguish. According to Segerstrale, they are separable on the setation of the second and third joints of the peduncle of the first antenna, and on the colour; *salinus* showing the banded colour pattern found also in the subspecies *zaddachi* but absent in *oceanicus*, and *salinus* having as a rule six tufts of setae on the ventral surface of joint 2, antenna 1 (only four in *oceanicus*), and at least three tufts on the ventral surface of joint 3 (only two in *oceanicus*). These figures exclude the apical tufts of hair at the distal ends of the joints.

On these criteria the Ungava Bay specimens belong to the subspecies *oceanicus*. Table I gives the counts for various diagnostic characters for six mature males and two mature females. These counts were made on large specimens, up to 36 mm. overall length. The number of joints in the flagellum of antenna 1 is lower than those given by Segerstråle (1947), who quotes 57 as the maximum number for the male (38 for the female) and 10 in the accessory flagellum. The Ungava Bay specimens differ also from the description given by Sexton (1942) for the species *zaddachi*, and agree with the descriptions of the

oceanicus form (Segerstråle, 1947; Spooner, 1951), in the depth of the sinus of the head, which is considerable, owing to the projection of the lower angles, and in the development of the dorsal humps on pleon 4–6, which approaches the condition found in *locusta*. These characters are illustrated in Figure 31. Specimens from Greenland in the Copenhagen collection agree with the Ungava specimens in both characters, also in the lower margin of pleon 3, which is straighter than in *G. z. zaddachi*. There seems to be much variation in the shape of the postero-lateral corners of pleon 3, which may be produced to a greater or lesser degree, even in adult individuals. In immature specimens the corners are more pointed, resembling those of *locusta*.

With the exception of the variations mentioned above, the Ungava Bay specimens agree with the descriptions of Sexton, Segerstråle and Spooner. The lateral lobes of the head are obliquely truncate, side-plate 4 is rounded, not

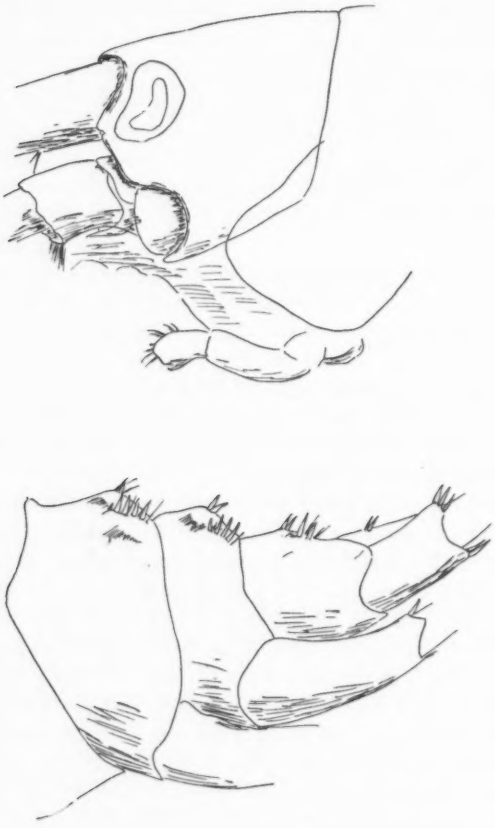

FIGURE 31. *Gammarus zaddachi oceanicus*, cephalon and pleon segments 4, 5 and 6. Male specimen, 31 mm. long.

TABLE I. Counts of diagnostic characters in *Gammarus zaddachi oceanicus*. In the last three columns, figures in brackets refer to setae, the others to spines. Horizontal rows bracketed together represent asymmetrical setation or spination, both sides of the animal being given. The numbers for the tufts of hair on the ventral surface of the peduncle of antenna 1 do not include the apical (distal) tufts on each joint.

Sex	Hair tufts, ant. 1, joint 2	Hair tufts, ant. 1, joint 3	Flagellum, ant. 1	Accessory flagellum	Spines on pleon segments			Telson spines and (setae)		
					4	5	6	Apical	Sub-apical	Sub-basal
♂	4	1	39	9	5-2-5	4-2-4	3-2-3	3 (5)	0 (1)	2 (0)
♂	4	1	40	9	4-2-4	4-2-4	2-2-2	3 (4)	0 (1)	2 (0)
♂	5	1	40	8	4-2-4	3-2-4	2-2-2	3 (3)	1 (0)	1 (0)
♂			38	8	4-2-3	4-2-3	2-2-2	3 (5)	0 (1)	2 (0)
♂	4	1	45	9	4-2-4	4-2-4	3-2-4	3 (3)	0 (1)	2 (0)
♂	4	1	39+		4-2-4	4-2-3	2-2-2	3 (6) 3 (4)	0 (0) 0 (2)	2 (0) 1 (1)
♀	4	1	41	7	5-2-5	5-2-4	3-2-3	3 (3)	1 (1)	2 (0)
♀	5	2	33	9 8	5-3-5	4-2-3	2-2-2	3 (3)	2 (1) 1 (1)	2 (0)

almost rectangular as in *locusta*, and the indentation of the frontal organ is of the *zaddachi* form. The peduncle of antenna 1 reaches just beyond the distal end of joint 4, antenna 2, which is a little shorter than described for *salinus*, but correct for *oceanicus*. The shape and spination of joint 6, per. 1 and 2, agree with *zaddachi* Sexton and with subspecies *oceanicus* Segerstråle, except that there are often only three spines instead of four at the angle of the palm in per. 2. In uropod 3, the inner ramus is four-fifths of the outer in length. The females do not appear to differ from the males in the diagnostic characters, except in the shape and spination of gnathopods, especially per. 2, in which the palm is more clearly defined and less oblique than in the male, and has no spine in the middle of its margin. The whole limb is smaller than in the male.

Owing to the taxonomic difficulties described above, the distribution of *Gammarus locusta* and *Gammarus zaddachi oceanicus* in North America and Greenland has not yet been fully established. The Copenhagen Museum collection contains large numbers of the genus, including specimens labelled "*Gammarus locusta* (L) sens. str." by Dr. K. Stephensen, from both coasts of Greenland. I have examined 132 of these specimens, and find that they all belong to *G. z. oceanicus*, some of them with certain slight variations mentioned below. Stephensen determined them before Sexton's (1942) paper appeared, and he was clearly interested at the time only in separating *Gammarus setosus* Dementieva from the others, which he labelled *G. locusta* "sensu stricto". He did the same with the Norwegian and Svalbard material, and some of the results of this work appeared in the third part of his study (1940a) of the amphipods of north Norway and adjacent waters, in which *Gammarus zaddachi* Sexton is tentatively equated with *G. wilkitzkii* Birula, and does not appear in the key to the species of *Gammarus* at all.

The Greenland specimens which I have examined in the Copenhagen collection were taken at Angmagssalik, Upernavik, Sakrak on the Vaigat, Ravns Storø, Lindenowfjord, Karajakfjord, Diskofjord, Nordre Strømfjord, Prøven, Clavering Island, Faeringerhavn, Sukkertoppen, Hvalrosodden, Danmarks Island, Kagssimiut (southwest Greenland), Kungmiut and Jakobshavn. Many of them were mature specimens. All of them agree in detail with the specimens from Ungava Bay. The shape of side-plate 4 in *G. z. oceanicus* is sometimes variable, occasionally approaching the more quadrate shape typical of *locusta*, and the depth of the expanded part is usually greater than in *G. z. zaddachi*, again a character found in *locusta*. One ovigerous female and three males, probably mature, in the Greenland specimens, showed a spination of the palm of per. 2 resembling the *locusta* pattern, in which the spines are arranged at evenly graded intervals (see Spooner, 1947). These are all minor variations from the typical *oceanicus* which do not disturb the determination of any of the specimens.

The evidence for the absence of *Gammarus locusta* from the coasts of Greenland and from Ungava Bay is thus considerable. As far as Greenland is concerned, this is also the conclusion of Spooner (1951) who appears to have examined some of the same material in the Copenhagen collection. The probability is that *G. z. oceanicus* is to be found everywhere along the coasts of

arctic and subarctic North America and that *locusta* does not occur in the north at all. *G. z. oceanicus* is now known from Novaya Zemlya, the Murman coast, Svalbard, the coasts of Norway, the Kattegat and the Baltic, Scotland, Iceland, east and west Greenland and the Canadian and United States eastern seaboard from Baffin Island to southern New England.

There is a point of interest in the fact that several of the divergences from *Gammarus zaddachi zaddachi* shown by *G. z. oceanicus*, and to a lesser extent by *G. z. salinus*, are in the direction of *G. locusta*. These are: (1) the shape of pleon 3, which is much straighter along the lower margin than in *G. z. zaddachi*; (2) the lesser setation of antenna 1; (3) the shorter peduncle of antenna 1; (4) the variability in shape of side-plate 4, which can sometimes strongly resemble the more square and deeper pattern of *locusta*; (5) the longer inner ramus of the third uropods, which can be four-fifths or more of the outer ramus; (6) the variability of the spine pattern on the palm of per. 2, which can sometimes resemble the *locusta* type; (7) the higher spine number on pleon segments 4–6; and (8) the greater development of the dorsal humps on pleon segments 4–6.

No doubt some of these resemblances, especially the lesser setation, can be put down either to the direct effect of the full salt-water environment in which both *locusta* and *oceanicus* live, or to an indirect effect of that environment manifested in a parallel evolution. In the southern part of the *oceanicus* range in Europe there is a large overlap with *locusta*. Nevertheless the resemblances are striking enough to suggest that *locusta* and *oceanicus* (and probably also *setosus* and *wilkitzkii*–see below) are northern derivatives from a common ancestor resembling *locusta* and living in full salt water, and that *salinus* and *zaddachi* are stages in a brackish-to-freshwater evolution from that ancestral form, an evolution which has taken place in the varied coastal environments of northwestern Europe.

Gammarus setosus Dementieva. (Fig. 32)

Syn.: *Gammarus locusta setosus* Stephensen, 1940a.

About 400 specimens of this species were collected, and in addition a large number of small immature individuals which could not be determined with certainty. Specimens were taken in the intertidal zone at stations 1A, 8, 65, 107A, 112, 201A, 205, 208B, 212, 215, 217, 224, 227 and 235. It was caught in plankton nets over very shallow water at stations 31 and 51. About 200 of the total number of specimens were taken in cod stomachs at Port Burwell, station 224, the only station at which the species was found in the cod. It was not taken in seal stomachs in Ungava Bay.

Gammarus setosus is closely related to *G. z. oceanicus*, being easily separated however by the rich endowment of feathered setae on peraeopods 5–7, pleon segments 4–6 and the telson. There is also a small number of less striking differences; the apical hairs on the telson are longer than in *oceanicus*, the ventral surfaces of antenna 1, peduncle joint 2 and 3, bear rather more hair tufts, and the hand of per. 2 is broader. All the differences except the abundance of feathered setae, even taken together, are not of any great significance, and moreover they are found to overlap with the *oceanicus* type. Add the fact that the two species are very often found together at the same stations, and the need

for breeding experiments becomes clear. There may be ecological differences separating the two, but the littoral collecting of the present series of expeditions was unfortunately not designed to bring such differences to light.

Stephensen (1940a) and Segerstråle (1947) both describe the posterolateral corners of pleon segments 2 and 3 as acute and produced, more so than in *G. zaddachi*. This is not the case in the Ungava Bay specimens, in many of which, especially the mature specimens, the corners of these two segments are almost quadrate (Fig. 32).

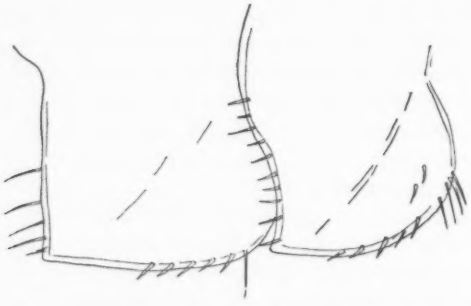

FIGURE 32. *Gammarus setosus*, epimeral plates of pleon segments 2 and 3. Adult male specimen.

The species is recorded from both arctic and subarctic regions: Winter Harbour, Cape Sabine, west and east Greenland, Jan Mayen, Iceland, Svalbard, north Norway and the Barents Sea, Novaya Zemlya and eastward to East Cape Siberia. It is recorded from Baffin Island up to Pond Inlet, and from Ellesmere Island: Craig Harbour (Ellis, unpublished); Alert Bay (in seal stomachs; McLaren, unpublished).

Gammarus wilkitzkii Birula

Seven specimens were taken in plankton nets at stations 7, 44, 57, 60 and 209. One specimen, 28 mm. in length, was taken in the intertidal zone at station 107B. In addition, nine specimens were found in the stomachs of ringed seals from station 29, from the mouth of the Koksoak River and in Leaf Bay, and seven were taken in cod stomachs at Burwell.

Gammarus wilkitzkii has been confused in the past with *G. locusta*. It is however immediately recognizable as distinct from all other species of the genus, even in quite immature stages, by the elongated third joint of the peduncle in antenna 1, and the long and abundant setae on the ventral surface of all three peduncle joints; also by the fact that the lateral groups of spines on pleon 4–6 lie farther back on the segments than the median groups. The spine number is also somewhat lower (in the present specimens 2-2-2; 3-2-3; 2-2-2 and 3-2-3; 3-2-3; 3-2-3). The spines themselves are longer than in other species. Furthermore, the pelagic habit is distinctive. (On the Siberian coast it appears to be found also in brackish water areas, which may explain the littoral record in

Ungava Bay at station 107B, at the mouth of a freshwater stream running across the beach.)

The tangled taxonomic history of the northern species of *Gammarus* is well illustrated by this species. First proposed as a variety of *G. duebeni* (Birula, 1897), it was raised to full specific rank by Gurjanova (1930). The following year it was proposed to make it a form of *setosus* (Dementieva, 1931), a suggestion repeated by Birula in 1937. Stephensen (1940a) considered it as possibly synonymous with *G. zaddachi*, and finally Sexton (1942) and Segerstråle (1947, 1948) confirmed Gurjanova's decision to make it a separate species.

G. wilkitzkii is probably circumpolar, predominantly arctic but also subarctic, known from Alert Bay, northern Ellesmere Island, Jones Sound and Winter Harbour, the east Greenland waters from Germania Land to Cape Farewell, Denmark Strait and the Greenland Sea, north Iceland, the waters of Svalbard and northern Norway, Barents Sea, Kara and Laptev Seas and along the Siberian coast to East Cape. It is possibly a good indicator of the presence of arctic water.

Gammaracanthus loricatus (Sab.)

One ovigerous female was collected at Port Burwell, close to low water mark at spring tide, August 8, 1948.

This is a shallow water arctic and subarctic circumpolar form, recorded from Hudson Bay (Shoemaker, 1926), Jones Sound (Sars, 1909), Prince Regent Inlet, Baffin Bay and Davis Strait (Ohlin, 1895), Collinson Point, Alaska, Bernard Harbour and Melville Island (Shoemaker, 1920), Lake Harbour (Dunbar, 1942), east and west Greenland, Svalbard, White Sea, Barents, Kara and Laptev Seas, New Siberian Islands and East Cape.

Family DEXAMINIDAE

Guernia nordenskiöldi (H. J. Hansen)

One male was taken in very shallow water in a plankton net at station 51.

This species was established by Hansen on specimens from West Greenland (Sukkertoppen and Christianshaab, in depths down to 60 fathoms), and it has since been recorded only in eastern Canadian waters. It was taken in the Gulf of St. Lawrence, when the male was found for the first time (Shoemaker, 1930a).

Family PHOTIDAE

Photis tenuicornis G. O. Sars

The material includes nine specimens of this species taken in the benthos at stations 18 and 202. The latter station produced two mature females on June 30, 1949, and at station 18 an almost mature female was taken on July 17, 1947.

The telson in the mature specimens lacks the setae and slight indentations figured and described by Sars (1895), but there is little doubt that the determination is correct.

The species is known mainly from the subarctic: north Norway, Franz Joseph Land, north and east Iceland and west Greenland (not east Greenland). This is the first record for North America.

Eurysteus melanops (G. O. Sars). (Fig. 33)

Twelve specimens were obtained at stations 18 and 226. Ovigerous females were taken at both stations, on July 17, 1947, and August 13, 1950.

According to Sars, the palm of per. 2 in both sexes is sinuous; in the present material only the immature females show this character. In the ripe females the palm is straight (Fig. 33).

FIGURE 33. *Eurysteus melanops*, per. 2, ovigerous female.

A subarctic and boreal species, taken also in the arctic, known from the Kara and Laptev Seas, White Sea, New Siberian Islands (Gurjanova, 1935b; Yashnov, 1948), Norway, Denmark (Stephensen, 1940a), west and east Greenland, Iceland. The record from the Gulf of St. Lawrence (Shoemaker, 1930a) probably applies to this species, but it is given under the name *E. maculatus*, as in Stebbing (1906), whose synonymy includes *E. erythrophthalmus*, a separate species.

Goësia depressa (Goës)

Taken at station 102, in the dredge; eight specimens including two females almost mature.

The species is new to North America. It is apparently predominantly subarctic, but is recorded from northeast Greenland (Franz Joseph Fjord and Scoresby Sound, in depths down to 54 metres (Stephensen, 1944a)); Novaya Zemlya (Barents Sea coast), Svalbard, west and east Greenland.

Protomedeia fasciata Krøyer

One ovigerous female and one immature female were taken in the dredge at station 33, August 10, 1947.

This species is of wide distribution, possibly circumpolar, and found in arctic, subarctic and boreal zones, known from the New Siberian Islands westward to Dolphin and Union Strait, but not yet recorded from east Greenland (Stephensen, 1942), south to the Gulf of St. Lawrence in North America and to the Skagerak and the Northumberland coast in Europe.

Protomedeia grandimana Brüggen

Eleven specimens were dredged at stations 20, 45 and 102. One very small specimen of the same genus was also taken at station 102, too small for certain determination. Six of the specimens, one male and five females, were close to maturity, caught on June 30, 1949.

This species is sometimes difficult to determine owing to the great changes that take place during the later moult stages, especially in the shape of per. 2 (Stephensen, 1942). The present specimens have been compared with specimens in the Copenhagen collection.

It is a predominantly subarctic species, but recorded also from the arctic: New Siberian Islands, Kara and Barents Seas, north Norway, Svalbard, Iceland, the southern tip of Greenland and eastern Baffin Bay. This is the first record from North America.

Family ISCHYROCERIDAE (Jassidae Stebbing, 1906)

Ischyrocerus nanoides (H. J. Hansen)

Five immature females were taken at station 102.

This is evidently not an abundant species. It has been recorded only from Baffin Bay, off west Greenland, and off the north of Svalbard (Stephensen, 1942). This is the first record for North American waters.

Ischyrocerus anguipes Krøyer. (Fig. 34)

Syn.: *I. minutus* G. O. Sars, 1895.

Several hundred specimens of this very common species were taken, both in the plankton and in the benthos. Planktonically the species was obtained at stations 1, 7, 18, 9, 31, 63, 103, 123, 124, 203, 206, 234 and 303; benthonically, at stations 58, 102, 203, 210 and 226. Ovigerous females were caught on the following dates: June 24 and 26, July 3, 11, 17, 18 and 20, August 10, 11 and 29, 1947; July 28, August 16, 1948; August 10 and 20, 1949; July 8 and 15, August 13 and 31, 1950; July 4, 1951. One female was taken from a ringed seal stomach on June 30, 1949, at Burwell.

Both Stebbing (1906) and Stephensen (1942) consider *I. anguipes* and *I. minutus* synonymous, the latter being a smaller and more southern form without the concave hind margin in joint 6, per. 2, in the male. Both forms of the species, if indeed they should be considered the same, were found in Ungava Bay, and there was considerable variation in the size of the ovigerous females. It is possible that the smaller ovigerous individuals belonged to the *minutus* form (the two are indistinguishable in the female), but the whole matter of size at

maturity in cold-water invertebrates is very complicated. A similar, and greater, range of size at maturity is found in *Ischyrocerus latipes* (below). The now classical work of Orton (1920) on the temperature characteristics of breeding in northern marine organisms may be relevant in this connection. Orton found that the onset of maturity could occur at almost any size once the environmental temperature rose above a critical minimum figure characteristic of each species.

There is a remarkable error in the description of this species in Sars (1895) which is repeated by Stebbing (1906). Both authors write that it is the inner ramus of the last uropods which carries the teeth on its upper margin; Stebbing even says "inner (not outer) rather broader, apically bent, having on upper margin 3 or 4 denticles". It is nevertheless the *outer*, not the inner ramus which is so formed.

FIGURE 34. *Ischyrocerus anguipes*, per. 2 of the male variant form described by Stephensen (1917), and found in Ungava Bay.

Stephensen (1917) described a variant of *I. anguipes* from southwest Greenland, having per. 2 shaped as in the female, although much larger, with longer antennae, and (in the male) peculiarly shaped joints in the peduncle of antenna 2. This variant also occurred among the Ungava Bay material (Fig. 34). Gurjanova (1934a) suggested that this variant was in fact identical with her new species *enigmaticus* from the Kara Sea, but with this I cannot agree. In all respects other than those mentioned the specimens in question (also Stephensen's specimens which I have examined) are typical *anguipes*, and are not in agreement with Gurjanova's description of *enigmaticus*. The shorter accessory flagellum, the serrated edge of the finger of per. 1, the form of the rami of uropod 3, and other characters place them unequivocally in *anguipes*. Moreover, I have a male specimen showing the variant antennae described by Stephensen but with the typical elongated hand of per. 2 of *anguipes* (*minutus* form), indicating that the species is variable and that other variants, or combinations

of variant characters, besides those described by Stephensen, are to be found.

This is an arctic and subarctic species, extending also into the boreal and known also from the southern hemisphere (South Africa and possibly Ceylon; for details see Stephensen, 1942). It is recorded from Bernard Harbour and Hudson Bay (Shoemaker, 1920, 1926), the Gulf of St. Lawrence (Shoemaker, 1930a), Labrador, Bay of Fundy, Cape Cod and Cape Hatteras, Jones Sound, west and east Greenland, Iceland and Jan Mayen, Svalbard, the whole Norwegian coast and the Kattegat, North Sea and British Isles, Barents, Kara and Laptev Seas and the Sea of Japan.

Ischyrocerus ?*megacheir* (Boeck)

One immature female, probably of this species, was taken at station 18.

The specimen is not mature, but has the long accessory flagellum of *megacheir*, the rami of the last uropods without denticles, and the gnathopods of the *megacheir* shape. The lateral angles of the head are almost acute, and pleon 3 rounded-quadrate.

An arctic and subarctic species, already recorded from Hudson Bay and the Gulf of St. Lawrence (Shoemaker, 1926, 1930a) and Hudson Strait (Dunbar, 1942); west and north Norway, Skagerak (Enequist, 1949), the deep water of the Norwegian Sea, west and east Greenland, Svalbard, White Sea, Jugor Strait and the Kara Sea, and the "far eastern seas" (Yashnov, 1948; probably referring to the Okhotsk and Japan Seas).

Ischyrocerus latipes Krøyer. (Fig. 35)

Syn.: ?*Ischyrocerus assimilis* (G. O. Sars).
?*Ischyrocerus pachtusovi* Gurjanova. New Synonymy.

Eighty-nine specimens were taken benthonically at stations 18, 33, 38, 102, 103, 203, 210, 226, 231 and 301. Ovigerous females were taken on August 13, 1950, at station 226. Two large males were taken in the stomach of a bearded seal off the mouth of Whale River.

There seems to be no reason to keep *I. latipes* and *I. assimilis* separate, and it is very probable that *I. pachtusovi* Gurjanova, 1933 (with figures in Gurjanova, 1935a), also belongs to the same species. The differences between *assimilis* and *latipes* which appear in the descriptions given by Stebbing and others do not appear in the specimens themselves, and after reviewing the whole of the Copenhagen Museum material of both species, and especially after *assimilis* has been redescribed by Stephensen (1944b), it appears that there is only one species involved.

In the descriptions in Stebbing (1906), the differences between *latipes* and *assimilis* are the following:

	I. latipes	*I. assimilis*
Head	lateral corners rounded	lateral corners sharp
Pleon 3	quadrate	obtusely rounded
Accessory flagellum (length relative to first joint of primary flagellum)	1:2	1:3
Per. 2 (male)	palm convex	palm straight
Per. 6	joint 2 broad	joint 2 oblong
Size	15 mm.	8 mm.

Given the known variability of species of *Ischyrocerus*, these are small differences in the first place, and examination of the Ungava Bay and Copenhagen material reveals that they are not correct, and that the original description of *latipes* (Krøyer, 1842) was inadequate. In specimens labelled *latipes* from Greenland, the lateral corners of the head have small sharp produced points; the accessory flagellum is much less than half as long as the first joint of the primary flagellum; the shape of the hand in per. 2 is indistinguishable from that of *assimilis* (both show the groove on the inner surface into which the finger fits), and the extent of the setation of the palm is related to the size of the animal; the shape of joint 2, per. 6, is variable, sometimes as broad and sometimes as narrow as the same joint in per. 5 and 7 respectively. A characteristic of both forms, one

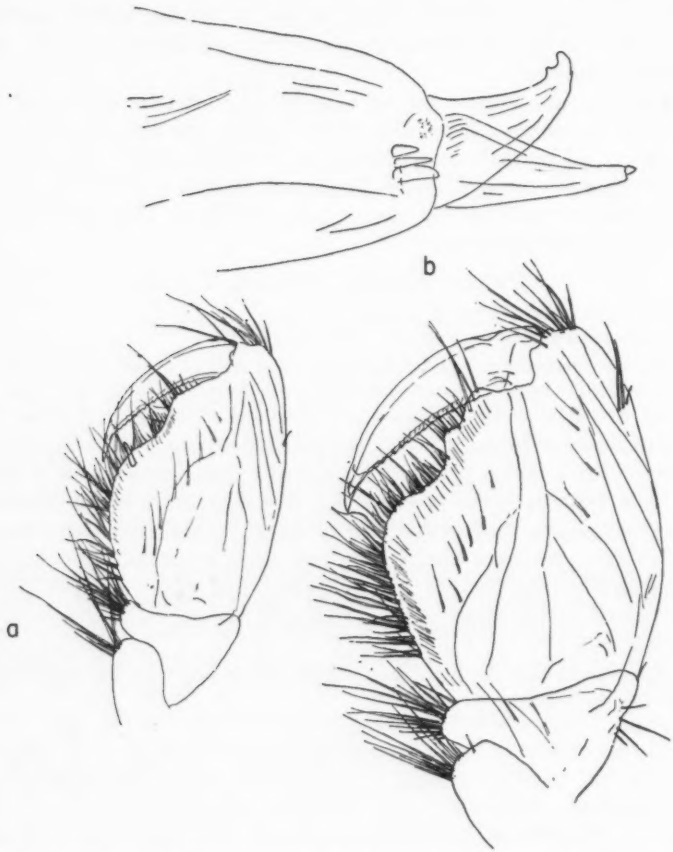

FIGURE 35. *Ischyrocerus latipes*. a: per. 2 of an ovigerous female of the *assimilis* form, from the *Ingolf* expedition material. b: per. 2 and third uropod of a typical female of *latipes* from Ungava Bay.

not found in other species of the genus, is the armament of the outer ramus in uropod 3 (Fig. 35) which consists of usually two, sometimes more, rather blunt denticles on the distal upper margin.

In the *Ingolf* report Stephensen (1944b) described specimens referred to *assimilis* which were slightly larger (9 mm.) than the specimens described by Sars, and differing in characters which strongly increase the probability of the identity of *latipes* and *assimilis*. In that material pleon 3 is quadrate, and the palm of per. 1, which is often sinuous in *latipes*, is also described as such in *assimilis*. Furthermore, the palm of per. 2 in the female has the indentation which is described by Hansen (1887) as characteristic of *latipes*, although the whole hand is somewhat slimmer than in the typical *latipes* (Fig. 35).

The description and figures of *Ischyrocerus pachtusovi* given by Gurjanova (1933, 1935a) are not quite detailed enough to make it possible to be sure of the identity of *assimilis* (as revised by Stephensen), *latipes* and *pachtusovi*, but the latter would appear to belong to the same complex. The accessory flagellum and the rami of the third uropods are not described, and there may be slight differences in the structure of per. 1. Most of the differences, however, which Gurjanova gives as distinguishing *pachtusovi* from *assimilis*, are nullified by the revised description of the latter species by Stephensen, particularly in the antennae, the second gnathopods and the shape of pleon 3. Differences in the structure of the head, the telson and the uropods, which Gurjanova mentions but does not amplify, are not apparent from the description. The length of *pachtusovi* is given as 17 mm. (male), which agrees with the present Ungava Bay specimens.

The conclusion reached tentatively here, on the base of the above study, is that there is only one species complex involved, consisting of three forms of very close affinity. *I. assimilis* G. O. Sars is a variety distinguished by slightly more slender build and with longer and slimmer antennae. This difference is more apparent in the female than in the male. In the male, the highly characteristic shape of per. 2 is the same throughout. The double row of setae on the ventral surface of the antennae is longer in the *assimilis* form, and no sign has been found, in the latter form (Copenhagen specimens) of the special sense organs at the base of these setae described by Schellenberg (1924) for *latipes*. Only a very few of these structures were present in the *latipes* specimens examined, both among the Copenhagen collection and in the Ungava Bay material. They appear to be easily lost in handling. No typical *assimilis* specimens were found in Ungava Bay.

The wide variation in size in the mature females in *latipes*, recorded by Hansen (1887) and observed also in the present collection from Ungava Bay, is possibly also a manifestation of the evolution of the species complex proposed here (but see also above, under *I. anguipes*, on the matter of size variation at maturity). *I. pachtusovi* Gurjanova, described from the Kara Sea, is very much larger than *assimilis* as heretofore described. Two large males in the Ungava Bay material agree in detail with Stephensen's 1944b) description of *assimilis*, but are the size of *pachtusovi* (15–16 mm.) and *latipes*. In short, the addition of material from the *Ingolf* expedition area, described by Stephensen as *assimilis*,

and of the present material from Ungava Bay, to the former known range of the group, makes it no longer possible to keep *assimilis* and *latipes* separate. And the agreement between these two forms and *pachtusovi*, on the basis of the present material and Gurjanova's description and figures, is exceedingly close, and covers the most striking and unusual structure and rich feathered setation of the hand of the second gnathopod in the male.

Ischyrocerus latipes Krøyer is recorded from west and east Greenland, Svalbard, Barents Sea, Kara and Laptev Seas and the New Siberian Islands. *I. assimilis* (G. O. Sars) is known from the deep water of the Norwegian Sea, Bear Island and north of Svalbard, and from Hudson Bay (Shoemaker, 1926). *I. pachtusovi* Gurjanova is known so far only from the type locality in the Kara Sea.

Ischyrocerus megalops G. O. Sars. (Fig. 36)

Fifteen specimens were obtained at stations 208 and 226. The material from the latter station included seven ovigerous females, August 13, 1950.

These specimens agree with the description and figures of Sars (1895) and with the specimens in the Copenhagen collection, from Norway and from the *Ingolf* expedition, except that they are noticeably more compact in general body

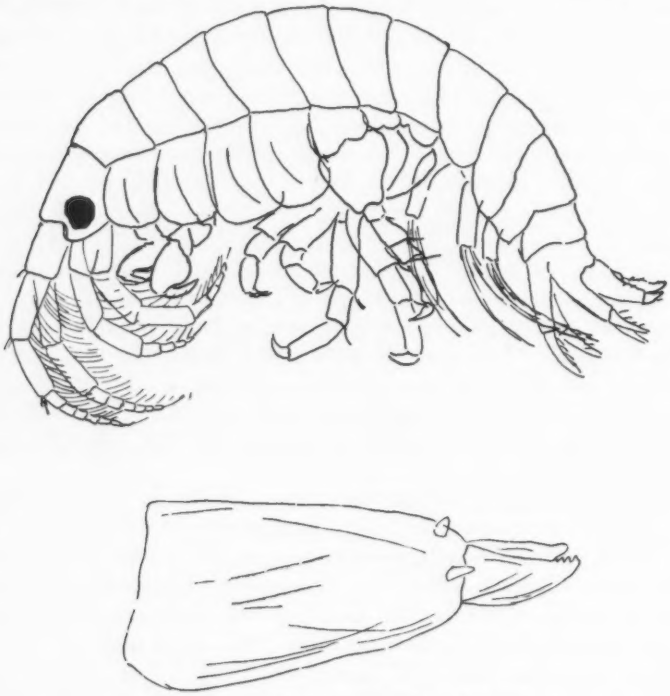

FIGURE 36. *Ischyrocerus megalops*. See text.

form, with antennae and per. 5–7 shorter and stouter. Perhaps the difference would justify the establishment of a subspecies, the more so since this is the first record of the species in North America. The uropod 3 illustrated in Figure 36 is atypical, lacking the terminal tooth. Normally the armature of the outer ramus is approximately the same as in *I. anguipes*.

This species has been recorded hitherto from north Norway, eastern Svalbard and Franz Joseph Fjord in northeast Greenland (down to 35 metres at the latter station–Schellenberg, 1935). It is thus apparently both arctic and subarctic in distribution.

Ischyrocerus commensalis Chevreux

Twenty-four specimens were taken in the benthos at stations 18, 102, 103 and 226; ovigerous females were obtained at the latter station on August 13, 1950.

Some of the immature individuals do not have the distinctive pair of tubercles at the distal end of the palm, per. 2, but show instead an undifferentiated wide protuberance. Shoemaker (1930a) says that the female of this species is at once separable from the *anguipes* female by the form of per. 2, but that the males of the two species are more alike. Nevertheless the males are also immediately separable, not only on account of the pair of tubercles on the hand of per. 2, but also because of the distinctive heel on the same segment, which is absent in *anguipes*. The rami of the third uropods, also, are much longer in *commensalis*.

This species is known chiefly from the subarctic: Gulf of St. Lawrence, off St. John's, Newfoundland (type locality, Chevreaux, 1900), west Greenland and two *Ingolf* stations in Denmark Strait off southeast Greenland, and from the Kara Sea (Gurjanova, 1935a, 1935b).

Family COROPHIIDAE

Ericthonius tolli Brüggen

One hundred and twelve specimens of this species were dredged at stations 11, 18, 20, 33, 102, 103, 106, 126, 201, 203 and 231; ovigerous females were taken on July 18 and August 8, 1947; September 2, 1948; June 30, July 6 and 7, 1949; July 8 and August 27, 1950. Two specimens were found in a bearded seal stomach from off the mouth of Whale River, and six in Atlantic cod stomachs at Port Burwell.

One variant specimen does not have the tuberculated palm typical of the species, but instead a broad lobate protuberance resembling the palm of *E. hunteri*; it is otherwise typical *tolli*. One male individual is asymmetrical in this respect, having the tuberculated palm on the right hand (per. 2) and the broader lobate structure on the left.

This species was first described by Brüggen (1909) from the Siberian shelf at longitude 147°27′E. It has since been recorded from the Laptev Sea (Gurjanova, 1932) and from the Kara, Chukchi and Japan Seas (Yashnov, 1948), Hudson Bay (Shoemaker, 1926) and north Baffin Bay (Stephensen, 1933), in depths down to 70 fathoms. Like *Paronesimus barentsi* this is probably a Pacific species which has spread a certain distance both west and east from the Bering

Sea, but has not yet achieved circumpolarity. Where found it seems to be fairly abundant.

Siphonoecetes typicus Krøyer

One specimen was taken at station 18, July 17, 1947.

This species has been redescribed from Krøyer's type material by Stephensen (1944a). The present specimen is in agreement with that description, except that the palm of per. 2 is not defined by an angle as figured by Stephensen from the type specimen. Other specimens in the Copenhagen material do not show this angle so well developed. The difference may be due to immaturity.

This is probably a subarctic species, known hitherto only from west and southeast Greenland (Stephensen, 1944a). This is the first record from North America. The species is very close to S. *colletti* Boeck.

Family PODOCERIDAE

Dulichia spinosissima Krøyer

Two ovigerous females were dredged at stations 33 and 203, on August 8, 1947, and July 8, 1950, respectively.

This species is apparently predominantly arctic in distribution, known from the White, Kara and Laptev Seas and east Svalbard, also the west coast of Baffin Bay. It is also recorded from present subarctic areas, as northwest Iceland, west Greenland between 60° and 72°N, and the Barents Sea. These latter records, however, were made before the recent warming of the marine climate, so that to consider this species as also of subarctic distribution might be misleading. Ungava Bay itself, on the other hand, is within the subarctic region, especially station 33, which is shallow and on the northeast side of the Bay.

Dulichia porrecta (Bate). (Fig. 37)

Eight specimens, including three males and one ovigerous female, were taken at stations 18 and 226, in the benthos. The mature female came from the latter station on August 13, 1950.

Figure 37 illustrates the development of per. 2 in the male, a most important diagnostic character. In immature individuals the hand is relatively much stouter than in the adult, there are two well-marked tubercles or lumps on the inner margin of the finger, joint 2 is short and the projection on the coxal plate is quite small and blunt. The distal tubercle on the finger is almost lost in the adult. In the immature condition the species strongly resembles *D. knipowitschi* Gurjanova (1933, 1934b), which Gurjanova (1936b) has equated with *D. aspina* Stephensen (1933). *D. knipowitschi* grows to a larger size then *porrecta*, so far as is known (a specimen 12 mm. long is in the Copenhagen collection), and does not develop the sharp process on coxal plate 2. Otherwise the two species are remarkably close.

The differences between *D. porrecta* and *D. spinosa* Stephensen (1944b) are exceedingly small. The latter species has a longer process on side-plate 2 than is at present known in *porrecta* and joint 2 of per. 2 is somewhat less

elongated. In the female, the joints of per. 1 and 2 are a little broader than figured for *porrecta* by Sars (1895), but the contrast with the actual specimens in the Copenhagen collection is less marked; in the Ungava Bay females, the width of these segments lies between *porrecta* and *spinosa* according to present descriptions, and the finger is fully half as long as joint 6, as described for *spinosa*. The only remarkable difference between the two species, if species they are, is the much greater depth at which spinosa was found (1,026 metres, *Ingolf*

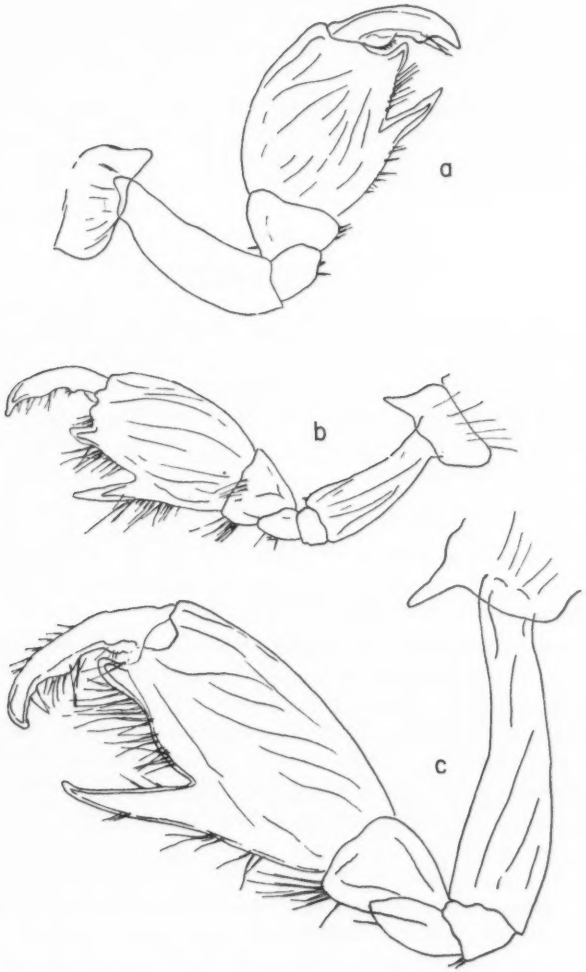

FIGURE 37. The development of the coxal plate and joint 6 of the second gnathopod in the male *Dulichia porrecta*. See text.

station 44). *D. porrecta* has not been recorded from depths greater than 120 metres.

Dulichia porrecta is subarctic and boreal, Atlantic and Pacific; known from the north Pacific (Chevreaux and Fage, 1925), Point Barrow, Alaska (Shoemaker, 1920), Hudson Bay (Shoemaker, 1926), west Greenland, Iceland, west and north Norway, north and east Scotland and northeast England, and the Danish waters (Stephensen, 1942).

Dulichia ?tuberculata Boeck

One male specimen, probably of this species, was taken in the plankton at station 101. It is not mature, but it is referred to this species on the basis of the single tubercle on the finger of per. 2.

This species is subarctic and boreal, like the foregoing species, but not known from the Pacific. It is recorded from the Gulf of St. Lawrence, west Greenland, west Svalbard, west and north Norway and the British Isles.

Sub-order ***Hyperiidea***

Family HYPERIIDAE

The sequence Gammaridea, Hyperiidea, Caprellidea, which is followed by Shoemaker (1930a) and by Stephensen (1935-42) is preferred to the older habit of placing the Hyperiidea first on the amphipod list. There seems to be little doubt that the Gammaridea represent the more primitive amphipod stock, and that the Hyperiidea and the Caprellidea are specialized, the former pelagically and the latter towards parasitism.

Hyperoche medusarum (Krøyer)

Syn.: *Hyperoche krøyeri* Bovallius (G. O. Sars, 1895).

Ten specimens were taken, all in the plankton, at stations 5, 13, 18, 41, 103, 222 and 231. A mature female was obtained on July 27, 1948, at station 5.

This is an arctic, subarctic and boreal species, and also bipolar, being known from the waters of South Georgia (Barnard, 1932). Recorded from the north Pacific (Monterey Bay), Alaska (Shoemaker, 1920), north, east and south coasts of Baffin Island (Dunbar, 1942), Norway, the Barents and White Seas and the Polar Basin (Yashnov, 1948), Svalbard, west and east Greenland, and generally in the north Atlantic "north of a line from the Gulf of St. Lawrence to south of Madeira" (Stephensen, 1944a); Japan Sea (Behning, 1939).

Hyperia medusarum (Müller)

Only two specimens of this species were obtained in the plankton at stations 13 and 57. Four were taken from cod stomachs at Burwell.

This species is predominantly subarctic in distribution, being unknown from east Greenland up to the present. No record of it from the Siberian shelf east of the Barents Sea has been found. It is known from the Pacific (Schellenberg,

1927; Holmes, 1908) including the Sea of Japan, and from Norway and Denmark, west Svalbard, the Faeroe-Shetland Channel and west of Ireland, Iceland, the Irminger Sea and southwest Greenland, Hudson Strait and Hudson Bay, Cumberland Sound, north coast of Alaska (Murdoch, 1885), Labrador (Smith, 1884), the Strait of Belle Isle (Bousfield, 1951) and the Gulf of Maine (Bigelow, 1926).

Hyperia galba (Montague)

Seventeen specimens in all, twelve taken in the plankton and five in cod stomachs at Port Burwell. The planktonic specimens came from stations 41, 44, 123 and 128. One ovigerous female was taken in this material, on August 24, 1949.

This species is also predominantly subarctic, but it is recorded from northeast Greenland and from the Angmagssalik area, and from the Siberian shelf; Barents Sea, Norwegian coasts, Svalbard, Iceland, Denmark Strait and the Labrador Sea, southeast Baffin Island, Hudson Bay, Strait of Belle Isle, Gulf of Maine. Also from the north Pacific and the Sea of Japan, probably circumpolar, and recorded from the antarctic.

Themisto abyssorum (Boeck)

Syn.: *Parathemisto oblivia* (Krøyer).

Thirty specimens were taken in the plankton at stations 1, 13, 18, 41, 128 and 231. All were immature.

The species is mainly subarctic but also arctic, and probably circumpolar. Known from Alaskan waters (Holmes, 1910; Shoemaker, 1920), Hudson Strait, Labrador (Dunbar, 1942), Strait of Belle Isle (Bousfield, 1951), Gulf of St. Lawrence (Shoemaker, 1930a), Gulf of Maine (Bigelow, 1926), Davis Strait and off southwest Greenland, east Greenland coast, Norwegian and Greenland Seas, Franz Joseph Land, Novaya Zemlya and the Siberian shelf east to 105°E (Brüggen, 1909).

Themisto libellula (Mandt)

Several thousand of this very abundant pelagic arctic species were taken in the plankton, at stations 1, 3, 7, 9, 13, 18, 33, 37, 41, 44, 53, 54, 56, 57, 60, 62, 63, 101, 103, 104, 106, 123, 125, 126, 128, 129, 201, 202, 206, 209, 211, 221, 226, 228, 231, 234, 301, 303, and 304. No mature specimens were caught. The specimens were taken at all depths from the surface to close to the bottom. It was also taken in numbers in seal stomachs and in the stomachs of Atlantic cod at Port Burwell.

Themisto libellula is arctic and subarctic, much more dominant in the former than in the latter, and can usually be relied upon as an indicator of arctic water. It becomes much less abundant in the southern parts of its range. It has been recorded from all arctic seas explored, and the most southerly records are the Strait of Belle Isle (Bousfield, 1951), off Cape Farewell and the southeast coast of Iceland (Stephensen, 1923), the Norwegian Barents and Murman Seas, Kara Sea, Bering and Okhotsk Seas (Behning, 1939). The Canadian Arctic Expedition of 1913–18 recorded it from several localities in the Canadian central and western arctic (Shoemaker, 1920).

Themisto gaudichaudi (Guérin)

Syn.: *Euthemisto compressa* G. O. Sars, 1895.
Euthemisto bispinosa G. O. Sars, 1895.
Parathemisto (*Euthemisto*) *gaudichaudi* Barnard, 1930, 1932.

Sixteen small immature specimens were caught planktonically at stations 18, 33, 41 and 44. They were taken only in 1947, not in any of the four succeeding seasons, a fact which may conceivably have some relation to variations in hydrographic conditions from year to year.

These specimens belong to the *compressa* form, following the scheme of Mogk (1927). The two forms were brought together to the same species by Stephensen (1924) and have since been shown to be identical with *T. gaudichaudi* (Barnard, 1930, 1932; Mogk, 1927). The species can be separated from both *libellula* and *abyssorum* even in very young stages. Long before the dorsal denticles develop, characteristics of *gaudichaudi* are the lack of the tuft of hairs on the finger of per. 5 (these tufts being characteristic of *libellula*), the longer finger on the same leg, the different armature of joint 6, per 5, the quite unequal rami of uropod 3 (almost subequal in *libellula*), the presence of a slight keel on the back on the segments which will later develop denticles, and a somewhat different body form, being more hunched anteriorly. *Themisto abyssorum*, even in young stages only 2 mm. long, is distinguished by the lack of elongation of per. 5, the lack of tuft of hair on the finger (as in *gaudichaudi*), and the armature of joint 6, per. 5.

T. gaudichaudi is found in both hemispheres in temperate regions, extending into the subarctic and subantarctic. It is rare in arctic water, but has been recorded from northeast Greenland and from Smith Sound (Stephensen, 1944a, 1933).

Sub-order ***Caprellidea***

Family CAPRELLIDAE

Aeginina longicornis (Krøyer)

Syn.: *Aegina echinata* G. O. Sars.
Aegina spinosissima Stimpson.

For full synonymy and discussion see Stappers (1911).

The material includes seventeen specimens of this species, dredged at stations 22, 33, 203 and 231, and taken in the plankton at station 201 at the surface. Ovigerous females were taken on July 8 and August 27, 1950. In addition to these, eleven specimens came from the stomach of a bearded seal, off the mouth of the Whale River, September 2, 1948.

This is widely distributed in the arctic and subarctic, found also in the boreal. Not yet recorded west of Jones Sound in arctic Canada, but known from the Siberian shelf. It has been recorded from the Gulf of St. Lawrence and south to Chesapeake Bay.

Caprella septentrionalis Krøyer

Ten specimens were taken at stations 1, 19, 37 and 40, all in the plankton, and two were dredged at stations 53 and 203.

The distribution is similar to that of the last species; arctic, subarctic and boreal, probably circumpolar.

DISCUSSION

The list of amphipod species at present known from Ungava Bay, and described in this paper, is given in Table II, together with certain details of maturity and distribution. The list contains 114 species, five of which are new to science, 21 (not including the new species) new to North America, and one new to eastern North America. Certain matters of general interest arising out of the material, zoogeographical and systematic, should be summarized here.

Zoogeography

Ungava Bay lies in the subarctic zone as defined in the introduction to this paper (see Fig. 38), and almost all the species listed here are known to be fairly widely distributed in the subarctic belt. A few more northerly forms, however,

Figure 38. The approximate limits of the arctic, subarctic (shaded) and northern part of the boreal zones as defined and used in the present paper.

TABLE II. Summary of the distribution of the species treated. The first column of data, following the specific names, gives the numbers of the months (June, July, August) in which ovigerous females were found in Ungava Bay. A query in the "circumpolar" means "probably circumpolar." Queries in the following two columns mean that the species is recorded from the arctic zone as here defined but that depth data are missing from the record.

	Ovigerous ♀ ♀ (months)	New for North America	Circumpolar	Arctic, above 25 m.	Arctic, below 25 m.	Subarctic	Boreal	Japan or Okhotsk Seas
1. *Opisa eschrichti*	7		?			x	x	J
2. *Onisimus edwardsi*			?	x	x	x	x	
3. *Onisimus plautus*	6, 7		?	x	x	x	x	
4. *Onisimus affinis*			x	x	x	(x)		
5. *Pseudalibrotus littoralis*				x	(x)	x		
6. *Pseudalibrotus glacialis*			x	x	x	x		
7. *Pseudalibrotus nanseni*			x	x	x	x		
8. *Paronesimus barentsi*		x				x		
9. *Orchomene macroserrata*						x		
10. *Aristias tumidus*			x	x	x	x		
11. *Anonyx nugax*	7		x	x	x	x	x	J
12. *Socarnes bidenticulatus*	7		?	x	x	x		J
13. *Socarnes vahli*			?	x	x	x	x	J
14. *Tmetonyx orchomenoides*		x				x		
15. *Orchomenella pinguis*	7		?	?	x	x	x	J
16. *Orchomenella minuta*	6		x	x	x	x	x	O
17. *Orchomenella groenlandica*				?	x	x		
18. *Stegocephalopsis ampulla*			x		x	(x)		
19. *Stegocephalus inflatus*	7		x	x	x	x	(x)	J
20. *Ampelisca eschrichti*	7		?	x	x	x	x	J
21. *Ampelisca macrocephala*	8		?	x	x	x	x	J
22. *Byblis gaimardi*	6, 8		?	x	x	x	x	J
23. *Haploops tubicola*	6, 7		x	x	x	x	x	J
24. *Haploops setosa*	8				x	x	x	
25. *Pontoporeia femorata*			x	x	x	x	x	J
26. *Pontoporeia affinis*	8					x	(x)	
27. *Gitanopsis arctica*		x				x		
28. *Metopa sinuata*		x			(x)	x	(x)	
29. *Metopa ?propinqua*						x	x	
30. *Metopa bruzelii*	7, 8			?	(x)	x	x	
31. *Metopa cariana*	8	x	?		x	x		J
32. *Metopa alderi*	7, 8				?	x	x	
33. *Metopa longirama*				x		x		
34. *Metopa norvegica*	7	x				x	x	
35. *Metopa nordmanni*	7	x				x		
36. *Metopa longicornis*		x			x	x	(x)	

TABLE II (*Continued*)

	Ovigerous ♀ ♀ (months)	New for North America	Circumpolar	Arctic, above 25 m.	Arctic, below 25 m.	Subarctic	Boreal	Japan or Okhotsk Seas
37. *Metopa invalida*	8	x				x		
38. *Metopa hearni* n. sp.	7, 8	x				x		
39. *Metopella nasuta*	7					x	x	
40. *Metopella neglecta*	7	x			(x)	x	(x)	
41. *Metopella carinata*	8			?	?	x		
42. *Metopella longimana*	8	x				x	(x)	
43. *Stenothoe brevicornis*	8	x				x	x	
44. *Odius carinatus*						x	x	
45. *Acanthonotozoma serratum*				x	x	x	x	
46. *Acanthonotozoma inflatum*			x	?	x	x		
47. *Pardalisca cuspidata*				x	x	x	x	
48. *Oediceros saginatus*				x	x	x	(x)	
49. *Paroediceros lynceus*			x	x	x	x		J
50. *Arrhis phyllonyx*			x	x	x	x	x	
51. *Westwoodilla brevicalcar*						x		
52. *Westwoodilla megalops*					?	x	x	J
53. *Aceroides latipes*			x	x	x	x		
54. *Bathymedon obtusifrons*	6, 8		?	x	x	x	x	J
55. *Monoculodes longirostris*	6		?	x	x	x		
56. *Monoculodes latimanus*	7			x	x	x		J
57. *Monoculodes edwardsi*						x	(x)	
58. *Monoculodes tuberculatus*				x	?	x	x	
59. *Syrrhoe crenulata*	6, 7			x	x	x	x	J
60. *Amphithopsis longicaudata*	7, 8					x		
61. *Halirages mixtus*						x		
62. *Halirages fulvocinctus*				x	x	x	x	
63. *Halirages megalops*	6, 7, 8			x		x		
64. *Apherusa glacialis*			x	x	x	x		
65. *Calliopius laeviusculus*			?	x		x	x	J
66. *Pleustes panoplus*				x	x	x	x	J
67. *Pleustes medius*					?	x		
68. *Parapleustes pulchellus*					x	x		
69. *Parapleustes boecki*	7	x		?	?	x		
70. *Parapleustes bicuspis*				?	?	x	x	
71. *Parapleustes assimilis*	7, 8			x	?	x	x	
72. *Parapleustes sinuipalma* n. sp.	7	x				x		
73. *Parapleustes glabricauda* n. sp.	7	x				x		
74. *Sympleustes olriki*		x				x		
75. *Sympleustes buttoni* n. sp.	8	x				x		

TABLE II (*Continued*)

	Ovigerous ♀ ♀ (months)	New for North America	Circumpolar	Arctic, above 25 m.	Arctic, below 25 m.	Subarctic	Boreal	Japan or Okhotsk Seas
76. *Sympleustes glabroides* n. sp.	8	x				x		
77. *Paramphithoe hystrix*			?	x	x	x	x	
78. *Atylus carinatus*			?	x	x	x		OJ
79. *Eusirus cuspidatus*			?	x	x	x		
80. *Rachotropis aculeata*	6, 7		?	x	x	x		J
81. *Rachotropis inflata*				x		x	x	J
82. *Pontogeneia inermis*	6, 7, 8			x	x	x		J
83. *Weyprechtia pinguis*			x	x	x	x		OJ
84. *Gammarellus homari*				x		x	x	
85. *Melita dentata*				x	x	x	x	O
86. *Gammarus zaddachi oceanicus*	6, 7		?	x		x	x	
87. *Gammarus setosus*	6, 7		x	x	x	x		
88. *Gammarus wilkitzkii*			x	x	x	(x)		
89. *Gammaracanthus loricatus*	8		x	x	(x)	x		
90. *Guernia nordenskiöldi*						x		
91. *Photis tenuicornis*	6	x				x		
92. *Eurysteus melanops*	7, 8			?	?	x	x	
93. *Goësia depressa*		x		x	x	x		
94. *Protomedeia fasciata*	8		?	x	x	x	x	
95. *Protomedeia grandimana*		x		?	?	x		
96. *Ischyrocerus nanoides*		x			x	x		
97. *Ischyrocerus anguipes*	6, 7, 8		x	x	x	x	x	J
98. *Ischyrocerus ?megacheir*					x	x	x	OJ
99. *Ischyrocerus latipes*	7, 8	x		x	x	x		
100. *Ischyrocerus megalops*	8	x		x	x	x		
101. *Ischyrocerus commensalis*	8				(x)	x		
102. *Ericthonius tolli*	6, 7, 8			?	x	x		J
103. *Siphonoecetes typicus*		x				x		
104. *Dulichia spinosissima*	7, 8				x	x		
105. *Dulichia porrecta*	8					x	x	
106. *Dulichia ?tuberculata*						x	x	
107. *Hyperoche medusarum*	7		?	x	x	x	x	J
108. *Hyperia medusarum*						x	x	J
109. *Hyperia galba*	8		?	x	x	x	(x)	
110. *Themisto abyssorum*			x	x	x	x		
111. *Themisto libellula*			x	x	x	x		O
112. *Themisto gaudichaudi*				(x)	(x)	x	x	
113. *Aeginina longicornis*	7, 8		?	x	x	x	(x)	
114. *Caprella septentrionalis*			?	x	x	x	x	

are rare in the subarctic and may therefore be called arctic species. The most obviously arctic forms are *Onisimus affinis, Stegocephalopsis ampulla* and *Gammarus wilkitzkii. Themisto libellula, Pseudalibrotus littoralis, P. nanseni* and *P. glacialis* also show strong arctic preference but are nevertheless abundant, though not dominant, in the subarctic.

Thirteen of the Ungava Bay species are restricted entirely or almost entirely to the subarctic zone, namely (new species excluded):

Orchomene macroserrata (Bay of Fundy, Ungava Bay).
Tmetonyx orchomenoides (southwest Greenland, Ungava Bay).
Pontoporeia affinis (as marine species: north Alaska, Bering Sea, Ungava Bay; relict in Baltic and in fresh water).
Gitanopsis arctica (north Norway, east Iceland, southwest Greenland, southern Novaya Zemlya, Ungava Bay).
Metopa invalida (Hammerfest, Ungava Bay).
Westwoodilla brevicalcar (west and south Svalbard, Finmark, northwest Norway, southeast Iceland, west Greenland, Hudson Strait, Ungava Bay, Gulf of St. Lawrence).
Monoculodes edwardsi (Woods Hole, Gulf of St. Lawrence, Ungava Bay, Hudson Bay).
Amphithopsis longicaudata (White Sea, northwest Norway, Iceland, Gulf of St. Lawrence, Hudson Bay, Ungava Bay, west Greenland).
Halirages mixtus (southeast Greenland, Ungava Bay).
Sympleustes olriki (west Greenland, Ungava Bay, Kara Sea?).
Guernia nordenskiöldi (west Greenland, Ungava Bay, Gulf of St. Lawrence).
Ischyrocerus commensalis (south Kara Sea, Denmark Strait, west Greenland, east Newfoundland, Gulf of St. Lawrence, Ungava Bay).
Siphonoecetes typicus (west and southeast Greenland, Ungava Bay).

The known distribution of some of these species, as will be seen, is restricted, and further work may well reveal arctic localities for some of them. It should also be mentioned that only one of them is known from the Pacific sector (*Pontoporeia affinis*). All the rest are restricted, so far as is known at present, to the Atlantic subarctic.

There is no strictly boreal species in the Ungava Bay list, but many of them extend south into the boreal zone. A category of special interest is formed of those species (36 in all) which are found in the subarctic and arctic (panarctic forms) and which, in the eastern Atlantic region, extend southward into the North Sea, the west and south coasts of Norway, and most of them as far as the Skagerak. This group, which is represented in Figures 39 and 40, includes the following:

Onisimus edwardsi, O. plautus, Anonyx nugax, Socarnes vahli, Orchomenella minuta, Stegocephalus inflatus, Haploops setosa, Metopa sinuata, M. propinqua, M. bruzelii, M. alderi, M. longicornis, Metopella nasuta, M. neglecta, M. longimana, Stenothoe brevicornis, Acanthonotozoma serratum, Odius carinatus, Pardalisca cuspidata, Arrhis phyllonyx, Monoculodes tuberculatus, Bathymedon obtusifrons, Syrrhoe crenulata, Calliopius laeviusculus, Pleustes panoplus, Parapleustes assimilis, P. pulchellus, Paramphithoe hystrix, Ranchotropis inflata, Gammarellus homari, Gammarus zaddachi oceanicus, Eurysteus melanops, Protomedeia fasciata, Ischyrocerus anguipes, I. megacheir, Dulichia tuberculata.

These species present an anomalous distribution, since they extend well

down into the boreal zone in the North Sea area and (in some cases) the coasts of the British Isles, but are not found south of the subarctic boundary on the North American side, the subarctic boundary being the limit of penetration of arctic water. This type of distribution in the Atlantic area is shown by very many species of other groups, including isopods, decapod crustacea, and even birds. The explanation is not immediately apparent, and cannot be discussed at length here. One possibility is that species with this distribution are relicts, in the North Sea area, of former colder climatic conditions in that region, perhaps early post-glacial.

The large number of Ungava Bay amphipods which are recorded from the Japan Sea or the Sea of Okhotsk are also very probably relicts. The two seas concerned are cold water areas, somewhat analogous to the Baltic, and there is little if any evidence of the invasion of arctic water into them at the present

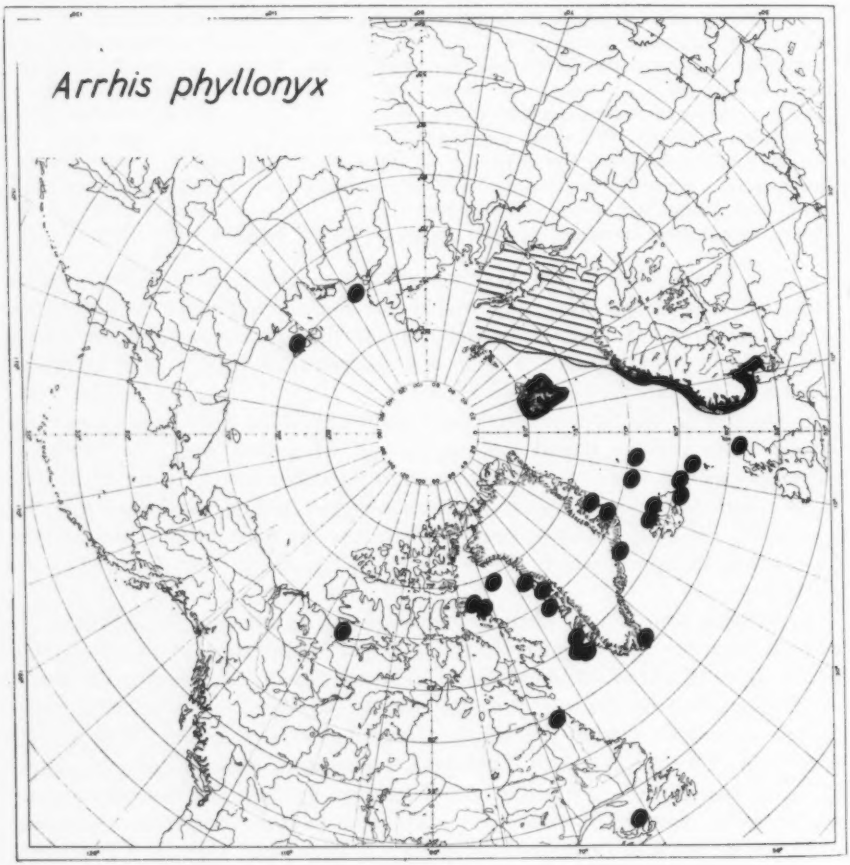

FIGURE 39. See text.

time. Altogether 32 of the present list of Ungava Bay species are known from one or other of these far eastern seas; the species themselves may be read off from Table II.

No less than 29 of the species so far found in Ungava Bay are not known from outside the region of Atlantic influence. They are thus not known to be circumpolar, and may be endemic to the Atlantic. In the list given here the new species described in this paper are not included. Four of the list, marked "K" are known from the Kara Sea but not from farther east. None of them is at present known from localities west of the Canadian eastern arctic, including Jones Sound and Hudson Bay. Most of them do not appear to have penetrated eastward beyond Novaya Zemlya: *Tmetonyx orchomenoides, Haploops setosa* (K), *Gitanopsis arctica, Metopa sinuata, M. propinqua, M. bruzelii, M. alderi* (K), *M. longirama, M. norvegica, M. invalida, Metopella nasuta, M. neglecta, M. carinata,*

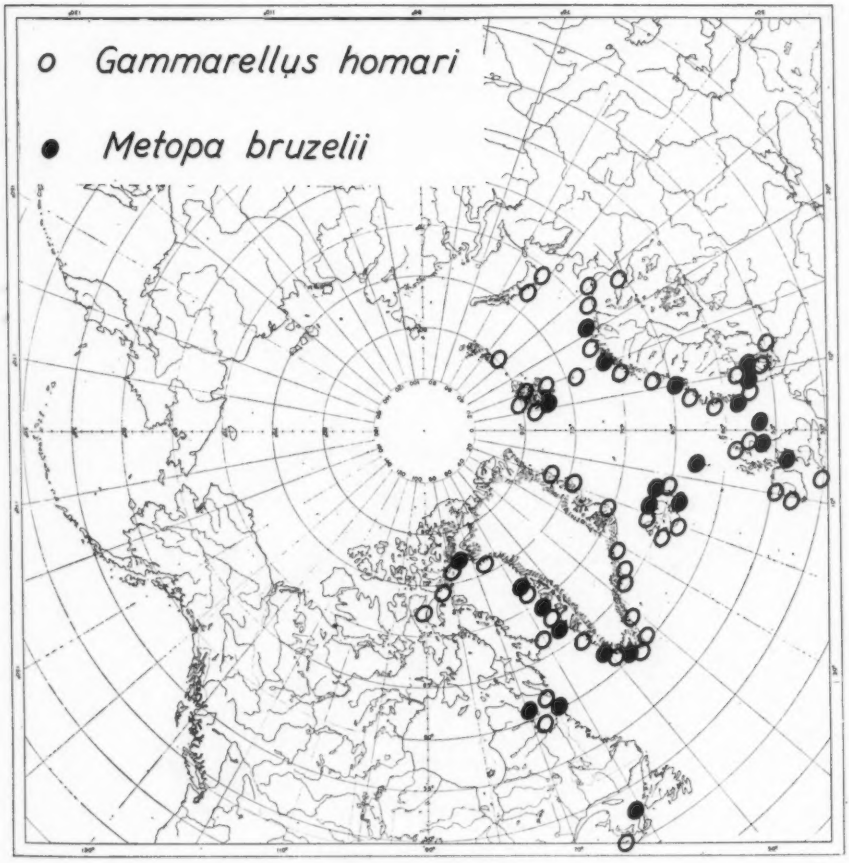

FIGURE 40. See text.

M. longimana, Stenothoe brevicornis, Westwoodilla brevi-calcar, Monoculodes edwardsi, Amphithopsis longicaudata, Halirages mixtus, Pleustes medius (K), *Gammarellus homari, Guernia nordenskiöldi, Photis tenuicornis, Goësia depressa, Ischyrocerus nanoides, I. megalops, I. commensalis* (K), *Siphonoecetes typicus, Dulichia tuberculata.*

Perhaps most interesting of all are the species which are apparently of Pacific origin and which have not yet penetrated far into the Atlantic area from either direction. These are not known west of the Barents Sea nor east of Greenland, and may be supposed to have followed dispersal routes from the Bering Sea, both westwards and eastwards, as suggested by Gurjanova (1935b). There are five such species, whose distribution is illustrated in Figures 41 and 42: *Paronesimus barentsi, Pontoporeia affinis, Metopa nordmanni, Pontogeneia*

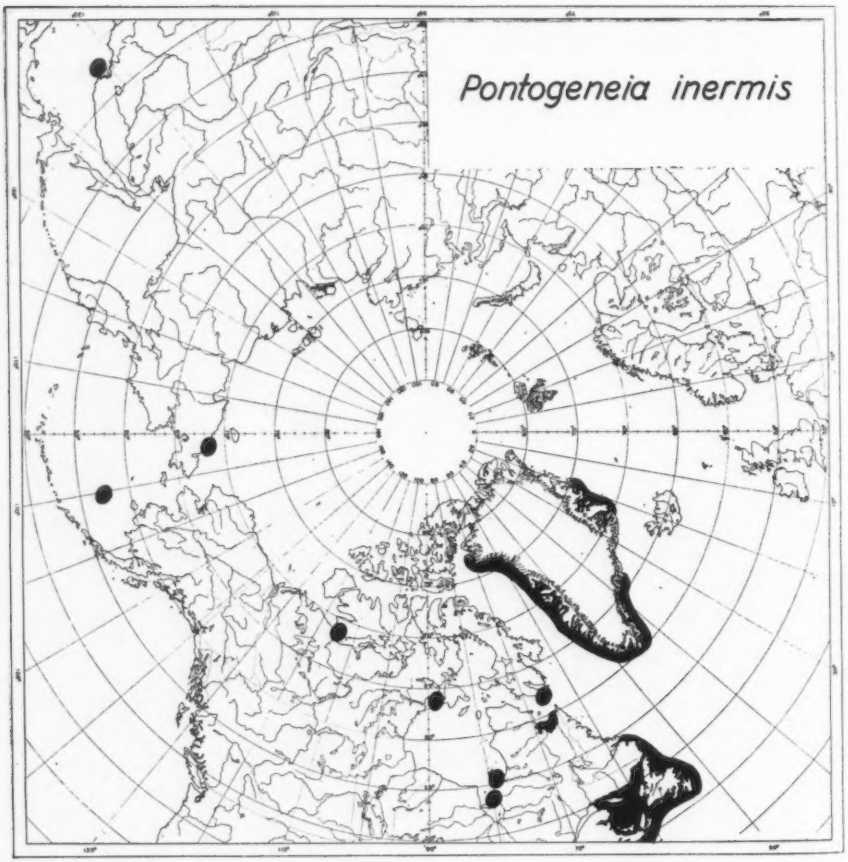

FIGURE 41. See text.

inermis and *Ericthonius tolli*. To these should be added the species pair *Orchomene macroserrata* Shoemaker and *O. tschernyschevi* Brüggen, which are very closely similar.

Many of the Ungava Bay amphipods which are found widely in the subarctic are also known from the arctic zone, and are therefore to be classified as panarctic. Among these panartic forms there is a small number which, according to their present known distribution, fall into the "low arctic" category of Lemche (1941), followed by Stephensen (1944a), defined as species which prefer summer temperatures between 0° and 7°C., distributed generally in the subarctic area and extending into the high arctic but only in the upper 25 metres, where summer temperatures, during the breeding season, are high. The number of such species in any one taxonomic group never appears to be very large.

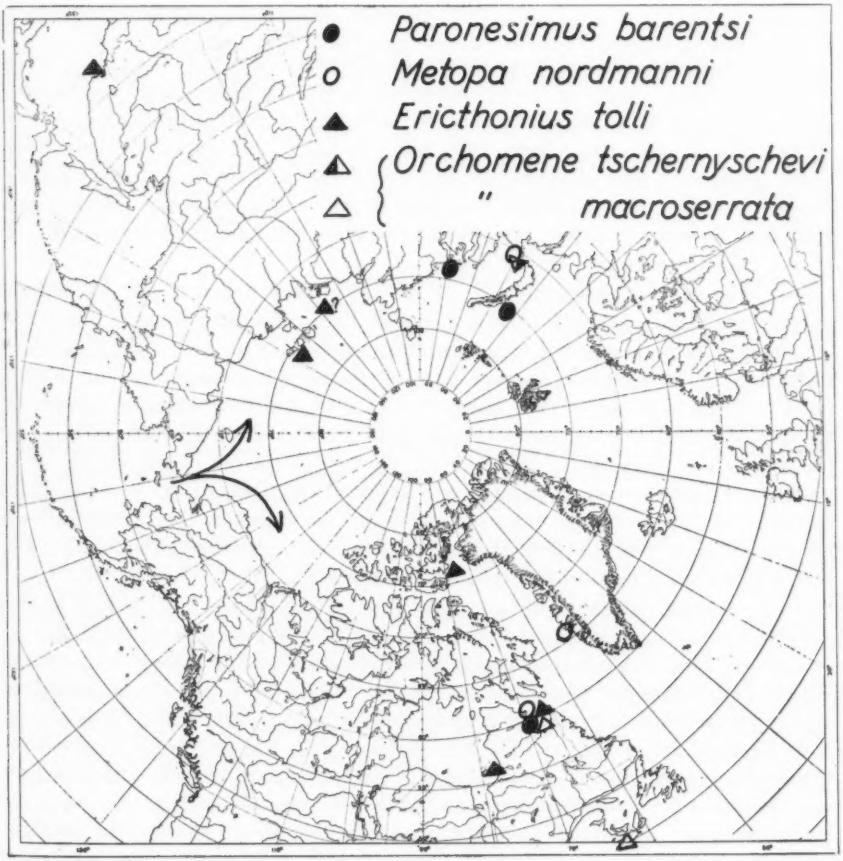

FIGURE 42. See text.

Lemche (1941) has two Opisthobranch molluscs out of 16 recorded from east Greenland; Stephensen (1944a) has 16, plus a similar doubtful number, out of 153 amphipods from east Greenland. As our knowledge of the distribution of these species advances, it is more than possible that deeper records will be made which will reduce the number still further. Of the 114 amphipods recorded from Ungava Bay, only four can be put in this category with reasonable certainty, as Table II shows: *Halirages megalops, Calliopius laeviusculus, Parapleustes assimilis* and *Rachotropis inflata.* If this "low arctic" group is really valid, it should perhaps properly be looked upon as a relict group in the arctic zone, remaining from a post-glacial slightly warmer period. For obvious reasons, planktonic surface forms and littoral forms are excluded from this group, since other ecological factors apply; this includes such species as *Metopa longirama, Gammarellus homari* and *Gammarus zaddachi oceanicus.*

Taxonomy

The eastern arctic and subarctic of Canada, indeed the whole of the Canadian waters, have not as yet been by any means thoroughly investigated. The great majority of marine animals, including amphipods, found in the waters of northern Canada are known from other parts of the north and have been described from types found in northern Europe and to a certain extent in Greenland. It follows that variations from the types, among specimens taken from Canadian waters, are to be expected; it would indeed be signally remarkable if at least slight variations were not found.

Besides the five new species described here, all of which belong to families (Stenothoidae and Pleustidae) of notoriously high variability, there is a number of variants from the typical form, the most noticeable of which are *Stenothoe brevicornis, Monoculodes longirostris* and *Ischyrocerus megalops.* In *Monoculodes longirostris* there is the suggestion of a typical rassenkreiss or artenkreis pattern of variation involving a species from the Kara Sea, *M. hanseni.* Among the benthonic amphipods, which have no pelagic larval development, such patterns of variation are to be expected in greater numbers as our knowledge of the full circumpolar fauna increases. As would be expected, the holoplanktonic amphipod species of the Hyperiidea offer far less taxonomic difficulty than do the predominantly benthonic and littoral Gammaridea.

The extension in the known range of some of the species has resulted, in the present work, in the bringing together of certain pairs or groups of species in synonymy. Thus evidence is brought forward which suggests that *Ischyrocerus latipes, I. assimilis* and *I. pachtusovi* are all variants of a single species complex; and in two cases, *Westwoodilla megalops* and *Haploops setosa,* the Ungava Bay material (and in the former case, also material from the Gulf of St. Lawrence) shows characters of two closely allied European forms hitherto described as separate species (*Westwoodilla megalops* and *W. caecula*; and *Haploops setosa* and *H. robusta*). These two pairs of species have therefore been brought together to single species, in which in each case the eastern Canadian form probably represents the common stock from which the European variants diverged.

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Tidal Currents in Juan de Fuca Strait[1]

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ABSTRACT

Three series of direct current observations taken in Juan de Fuca Strait in 1952 have been analysed. A linear relationship between the difference in sea level on the ocean coast and the Strait of Georgia and tidal currents has been shown. This relation holds from the surface to the lower depths. The current velocities in a cross-section can be predicted at any time. These sections show that the ocean water tends to intrude along the bottom on the flood, expanding upward and favouring the southern shore. The ebbing water is first noticed in the middle of the strait, then it expands down and across favouring the northern shore. The ebb current is stronger at the surface, and the flood current stronger near the bottom. Surface current predictions are shown to be comparable to the U.S. Coast and Geodetic Survey tidal predictions. From this it is reasonable to believe that the predicted tidal currents at the lower depths should also be valid.

INTRODUCTION

During 1952 several series of current observations were made in Juan de Fuca Strait to determine the nature of the tidal velocity cycle at the surface, at mid-depth, and near the bottom, at three stations (A, B, C, Fig. 1) in a line across the strait. The measurements were made every half-hour, for thirty hours at each station, during a spring tide cycle, and also during the neap tide cycle of the following or preceding week. Series of observations were made in the early spring, mid-summer, and late autumn.

The surface current observations are the most complete and have been discussed in a previous paper (Herlinveaux, 1954). Owing to failures in the current meters the deep current measurements were not successful during the spring and summer observations. However the autumn data, which are the basis of this paper, are complete (Table I).

In the previous paper it was shown that the surface tidal currents are reversing, and are proportional to the difference of tidal height from Clayoquot, on the ocean coast, to Point Atkinson, in the Strait of Georgia. Since the predicted tides are published (Tide Tables for the Pacific Coast of Canada) for both of these reference stations, it was possible to provide a simple rule for prediction of the velocity and direction of these currents. It was also shown that the ebb flow was stronger and endured longer than the flood, at all times of the year, and did not appear to be related to the freshet. In fact, the scatter of the data was not increased when the data for the spring and neap tides and the spring, summer and autumn were superimposed.

In the study of the deep currents it was anticipated that a similar linear relationship would be found between the deep tidal currents, and the difference

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FIGURE 1. Juan de Fuca Strait and vicinity showing Stations A, B and C where velocity observations were made; and the tidal reference stations at Clayoquot, Victoria and Point Atkinson.

TABLE I. Catalogue of current measurements in Juan de Fuca Strait during October 1952.

STATION A

First Series 0815, 17 October to 0756, 18 October 1952.
Latitude 48° 21′ N, Longitude 123° 56.2′ W.
Neap tide range 9.0 feet.
Depths observed 0, 15, 210, 420 feet.

Second Series 0315, 23 October to 0600, 24 October 1952.
Latitude 48° 21.2′ N, Longitude 123° 57′ W.
Spring tide range 12.1 feet.
Depths observed 0, 15, 210, 360 feet.

TABLE I (*Continued*)

STATION B
First Series 1820, 14 October to 0016, 16 October 1952.
Latitude 48° 17.5′ N, Longitude 123° 58.4′ W.
Neap tide range 7.5 feet.
Depths observed 0, 15, 240, 480 feet.
Second Series 1815, 20 October to 2353, 21 October 1952.
Latitude 48° 18.1′ N, Longitude 123° 59.5′ W.
Spring tide range 11.6 feet.
Depths observed 0, 15, 270, 540 feet.
STATION C
First Series 0103, 16 October to 0605, 17 October 1952.
Latitude 48° 14′ N, Longitude 124° 00′ W.
Neap tide range 8.0 feet.
Depth observed 0, 15, 210, 420 feet.
Second Series 0100, 22 October to 0200, 23 October 1952.
Latitude 48° 13.8′ N, Longitude 124° 00.3′ W.
Spring tide range 12.3 feet.
Depths observed 0, 15, 210, 360 feet.

of sea level from the ocean to the Strait of Georgia. It was also believed that the flood current would become more dominant with depth. The lack of spring and summer data is regretted, but it has been shown that the seasonal variation of the tidal cycle is negligible at the surface, and it is unlikely that these effects would appear in the sub-surface currents. Therefore, it is reasonable to believe that the October data are representative of the tidal current phenomena.

PROCEDURE

The ship was secured with a single bow anchor and allowed to swing with the tide. Since the winds were absent or light, there was little or no tendency to yaw or sail to the anchor. Measurements were made with a standard Ekman current meter (Ekman, 1932). Care was taken to take these measurements when the ship rode steady to anchor. During periods of maximum current the meter and suspension line trailed aft in the current, even though heavy weights were used. However, credible readings were obtained continuously and these have been accepted.

ANALYSIS OF THE OBSERVED TIDAL CURRENTS

The hodographs shown in Figure 2 illustrate the character of the tidal flow in this area. Vectors drawn from the origin to the points in the diagram represent the observed velocity and direction of the current. The lines connect successive observations, and indicate the sense in which the current changed. These diagrams suggest that the tides in this area may be rotary. However, the tendency is confused. The direction of rotation is not always consistent. The current changes from flood to ebb and back again through a southward arc, and for no apparent

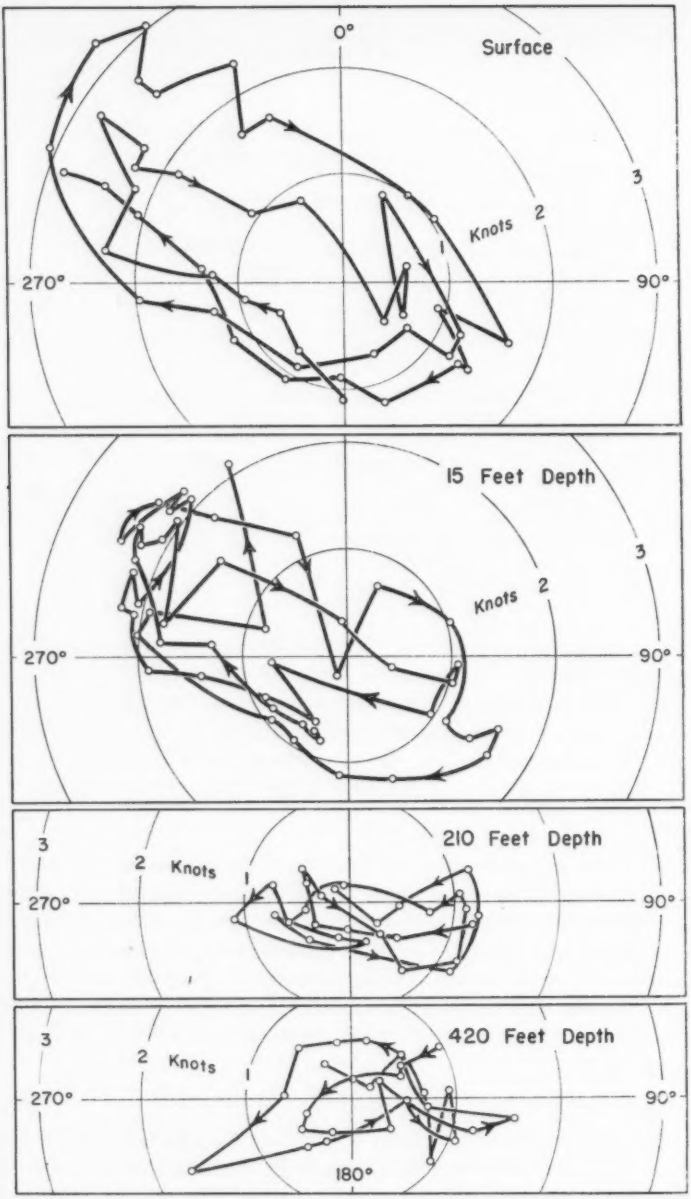

FIGURE 2. Hodographs of the hourly current vectors at Station C, from 1500, October 17 to 1900, October 18, 1952. Vectors drawn from the origin to the points in the diagram represent the observed velocity and direction of the current. The heavy lines connect successive observations and the arrow points indicate the sense in which the current direction changed.

reason may change through a northward arc on the next cycle. The Figure illustrates one of the simplest series of data, the others are considerably more confusing. It was not possible to make a reasonable analysis on the basis of rotary currents.

In general, the maximum currents occurred when the flow was seaward (ebb) or when it was into the strait (flood), and the occurrence of these maxima was regular. The velocities associated with cross-channel flow were real, but were generally small, and occurred at times associated with a hypothetical condition of slack water. Because of this the data have been analysed as simple reversing currents.

As in the previous study, the velocity of the tidal flow is related to the difference of sea level between Clayoquot on the ocean coast, and Point Atkinson in Georgia Strait. It would appear more logical to relate the velocities to tidal differences in Juan de Fuca Strait, closer to the scene of current measurements. However, this was not practical because the tides at the inner end of the strait are not completely defined in the Tide Tables. Thus, even if the relations of velocity to tidal difference were determined from tidal records, they could not be used for prediction of the currents from the predicted tides.

Figure 3 illustrates the tides at the reference stations, the difference of sea level between them, and the tidal current data observed during one day, at Station C, on the south side of the strait. This Figure is representative of all the data.

TABLE II. The relations between the current velocities (V, in knots) at specific depths at Stations A, B and C in Juan de Fuca Strait, and the difference of tidal height (ΔH) from Clayoquot to Point Atkinson.

Depth	Time lag	Relation	Probable error
feet	*minutes*		*knots*
		STATION A	
0	140	$V = 0.2\,\Delta H - 0.4$	± 0.3
15	150	$V = 0.2\,\Delta H - 0.6$	± 0.3
210	120	$V = 0.2\,\Delta H - 0.2$	± 0.3
390	180	$V = 0.2\,\Delta H + 0.1$	± 0.2
		STATION B	
0	130	$V = 0.2\,\Delta H - 0.8$	± 0.3
15	120	$V = 0.2\,\Delta H - 0.9$	± 0.3
255	180	$V = 0.2\,\Delta H + 0.1$	± 0.2
480	180	$V = 0.2\,\Delta H + 0.2$	± 0.2
		STATION C	
0	120	$V = 0.2\,\Delta H - 0.2$	± 0.5
15	120	$V = 0.2\,\Delta H - 0.2$	± 0.4
210	150	$V = 0.2\,\Delta H + 0.3$	± 0.2
390	150	$V = 0.2\,\Delta H + 0.2$	± 0.3

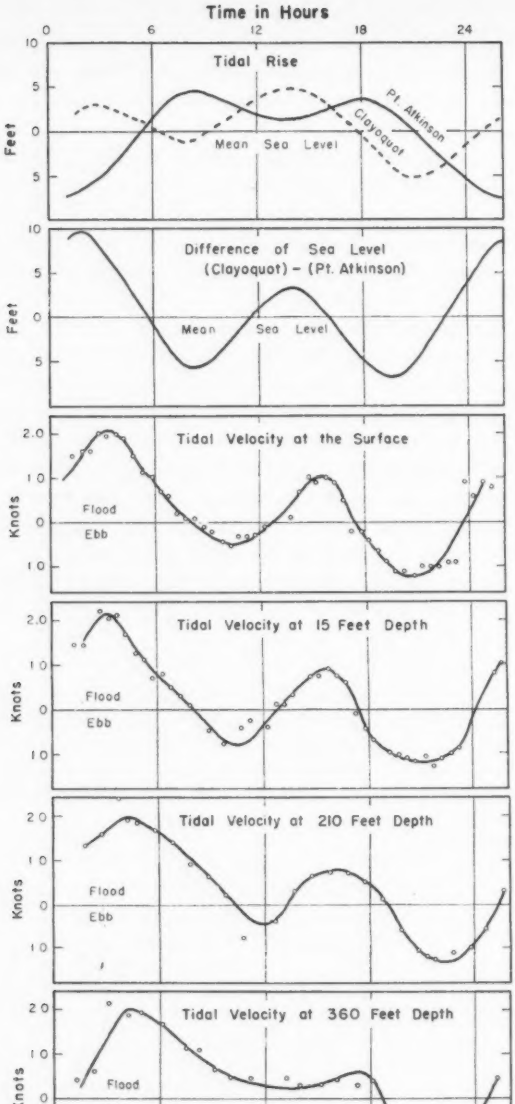

FIGURE 3. The tidal rise at Clayoquot and Point Atkinson, the difference of tidal height between these points, and the tidal current data at the surface, 15, 210 and 360 feet depth at Station C, October 22, 23, 1952.

The tidal currents wax and wane and reverse direction in a cycle of the same period as the sea level diffrence between the ocean and the Strait of Georgia. When the time scales of the tidal current curves were shifted so that the tidal and current maxima coincided, it was found that the velocity (V) was approximately a linear function of the difference of tidal height (ΔH) of the form

$$V = K\,\Delta H + C \qquad (1)$$

These relations are illustrated in Figure 4. The time lags, the equations of the relations, and the probable errors are shown in Table II.

This relation has the form of a wave equation which implies that the velocity is associated with a progressive tidal wave advancing along Juan de Fuca Strait which wave has been discussed by Bauer (1928) and Redfield (1950). This definition of the tidal currents in Juan de Fuca Strait is in distinct contrast to the hydraulic tides in Seymour Narrows at the northern end of the Strait of Georgia (LaCroix and Tully, 1954), where the head is proportional to the square of the velocity.

As might be expected from the character of the data as shown in Figures 2 and 3, the greatest error approaches 0.5 knot and is associated with the periods of change of tidal direction. For predictions greater than one knot the probable error seldom exceeds 0.2 knot. Certainly some part of this error can be attributed to the measurements, but as will be shown later it may be regarded as natural variations due to the mechanism of the system.

The functions are the same during spring and neap tide cycles, that is, they are independent of the range of the tide. The ebb bias decreases with depth, vanishes at mid-depth, and at the bottom the flood is stronger and endures longer than the ebb. Figure 4 indicates the similarity of the tidal phenomena at all depths, but does not include the time lag which is different at each position.

In order to visualize the flow through the cross-section (A, B, C) the series of predicted hourly velocity profiles, shown in Figure 5, have been constructed for June 10, 1952. This date was chosen because it was a period of spring tides when the diurnal inequality was large. Thus the sequence of 25 profiles for the tidal day (24 hours, 52 minutes) illustrates the velocity cycles through large and small tidal ranges.

In general, the flow is in the direction of ebb or flood, from surface to bottom. The ebb is always strongest near the surface, whereas the flood is stronger in the depths. About two hours is required for the flow to turn from flood to ebb or vice versa. During this period both flood and ebb currents exist in the strait. The flood first appears near the bottom on the southern side. It expands across the strait and upwards, and always favours the southern side. The ebb first appears in the middle of the strait at the surface, and expands to both sides and downwards, favouring the northern side.

The tendency of the currents to veer to the right and favour the southern side during the flood, and the northern side during the ebb, may be attributed to the Coriolis Force, consequent on the earth's rotation.

The fact that the ebb is predominantly a surface flow and the flood a deep flow may be explained by the principles enunciated by Tully (1953) in his discussion of the behaviour of fresh water entering the sea. The ebb flow which carries sea water mixed with fresh water from the Strait of Georgia is less dense

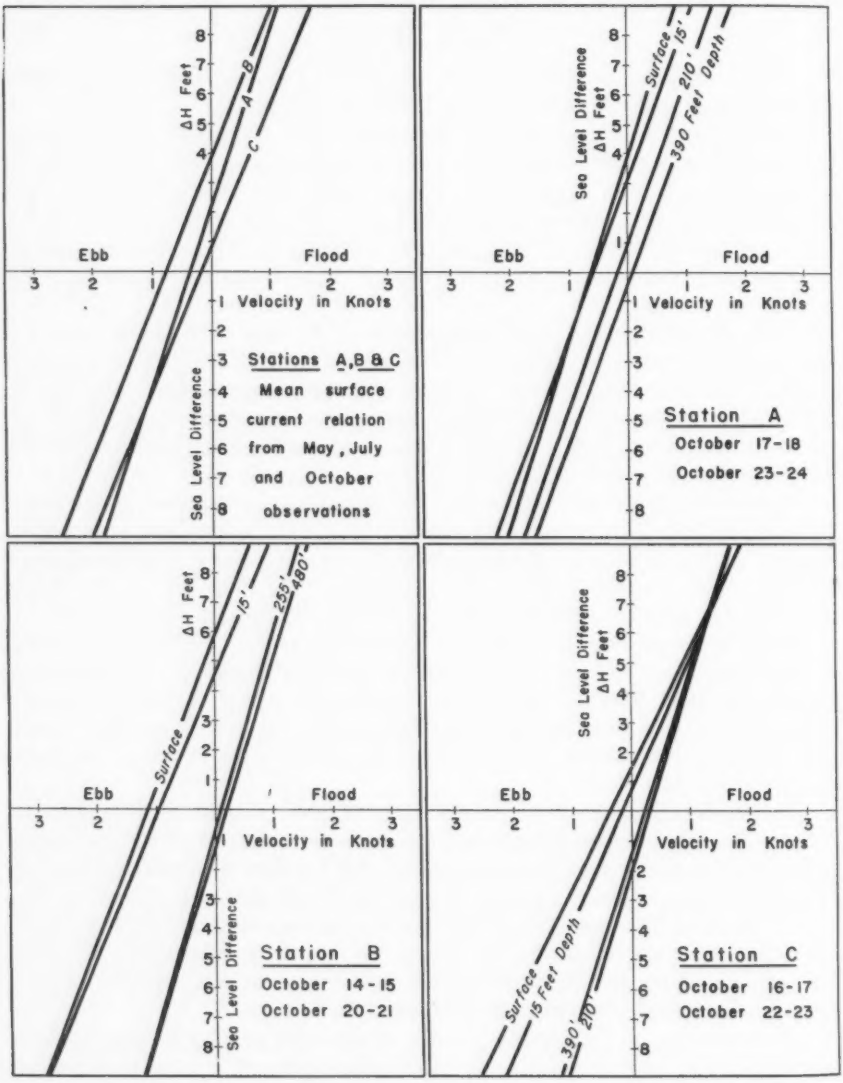

FIGURE 4. The relation of the difference of tidal height to the current velocities. Each function represents the relation at one position and one depth.

than the flooding waters intruding from the ocean and tends to overrun them. Thus the currents are segregated because of the difference of density of the water masses.

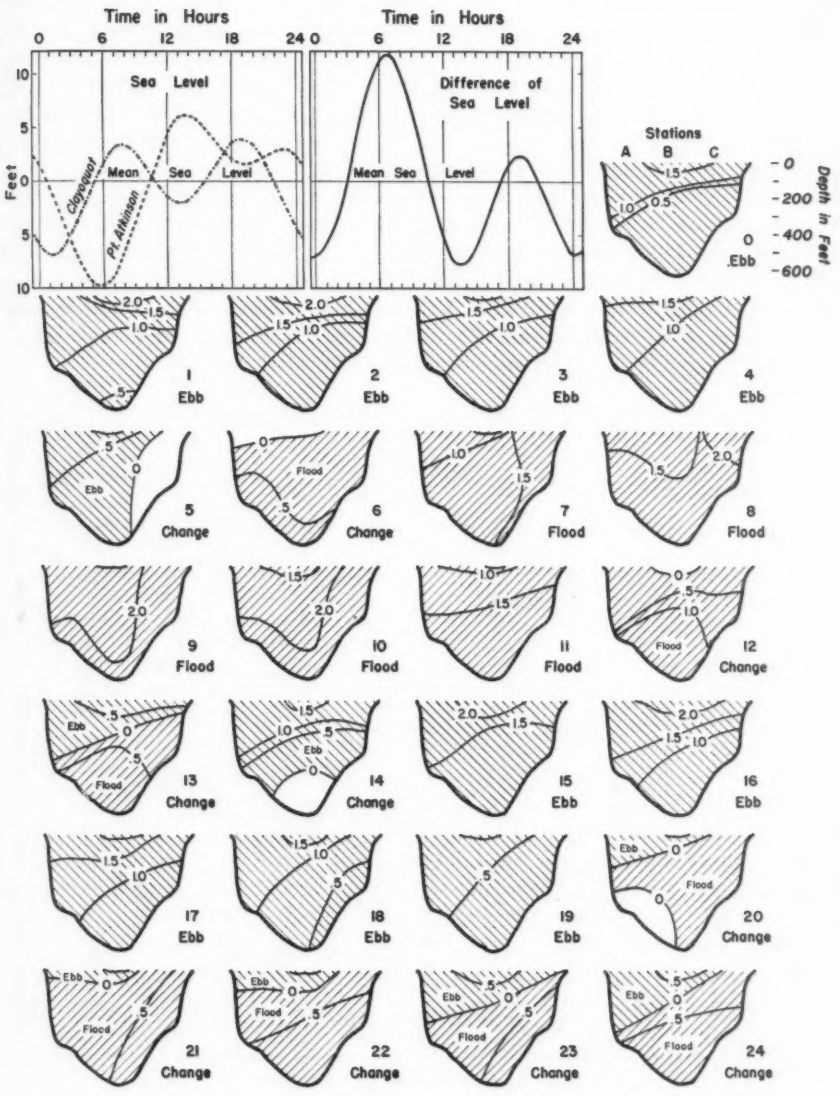

FIGURE 5. Calculated tidal heights at Clayoquot and Point Atkinson, June 10, 1952, the resulting difference in sea level during spring tides, and the consequent calculated hourly current profiles through the cross-section A, B, C, in Juan de Fuca Strait. Velocity in knots.

There is a lag of about two hours and ten minutes between the maximum difference of sea level, from the ocean to the Strait of Georgia, and the maximum current, through the observed section (A, B, C). Bauer (1928) showed that the tide was a progressive wave advancing along Juan de Fuca Strait at about 30 miles an hour. It may be expected that the point of maximum velocity resulting from this wave will also progress along the strait. No doubt it would be possible to find reference points such that the sea level difference and current would be exactly in phase, but these are not listed in the Tide Tables. The rate of progress of the point of maximum velocity may be deduced from the Current Tables of the United States Coast and Geodetic Survey (1952). These show that the current cycle at Pillar Point, near Station C, lags 30 minutes after the current at Neah Bay at the entrance to the strait, and a further lag of 25 minutes is noted from Pillar Point to Port Angeles. On the basis of these data, and the results of our study, a predicted co-tidal chart of maximum velocity (and presumably of slack water) in Juan de Fuca Strait has been constructed as shown in Figure 6. It is probable that this chart is nearly correct but its reliability cannot be guaranteed without some further observations.

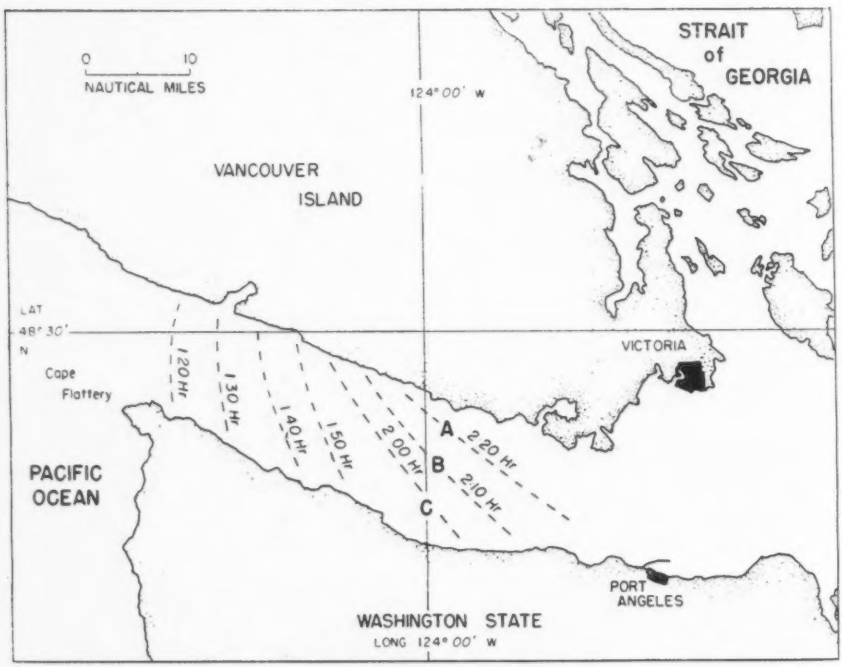

FIGURE 6. Co-tidal chart of surface tidal currents in Juan de Fuca Strait, showing the lag of maximum tidal current after the maximum difference of sea level between Clayoquot on the ocean coast, and Point Atkinson in Georgia Strait.

In Table III the predicted times of slack water and maximum currents at Pillar Point, from the Current Tables, are compared with observed velocities, and the predictions at Station C, according to the rule developed in the previous paper. Examples were selected in March, July and October, to encompass representative seasonal variations. The predictions in the Current Tables do not agree well with the observed data or with our prediction. As compared with our observed data, the Current Table predictions for the ebb current appear to be about the same; however, the predictions for the flood current and times of slack water differ significantly. Since the method used by the U.S. Coast and Geodetic Survey in obtaining their predictions has not been studied, these differences will not be discussed here.

TABLE III. Example of observed and predicted times of surface tidal currents at Station C in Juan de Fuca Strait.

Date 1952	Tidal current stage	Predicted by the rule		Predicted from U.S. Geodetic Current Tables		Observed Surface current	
		Time	Velocity	Time	Velocity	Time	Velocity
			knots		*knots*		*knots*
March 11	Slack	2315	0	0032	0	2340	0
March 12	Max. Flood	0215	1.5	0242	0.7	0230	1.3
	Slack	0515	0	0456	0	0512	0
	Max. Ebb	0845	1.7	0901	1.9	0845	1.4
	Slack	1150	0	1304	0	1150	0
	Max. Flood	1440	1.3	1503	0.6	1415	1.4
	Slack	1730	0	1710	0	1720	0
	Max. Ebb	2045	1.6	2212	1.8	2045	1.7
	Slack	2350	0	0108	0	0015	0
	Max. Flood	0245	1.4	0310	0.6	0300	1.3
July 6	Slack	1650	0	1705	0	1630	0
	Max. Ebb	1950	1.6	2020	1.2	1935	1.1
	Slack	2340	0	....	..	2250	0
	Max. Flood	0100	0.4	0114	..	0100	0.8
	Slack	0230	0	....	..	0250	0
	Max. Ebb	0645	2.0	0733	2.3	0700	2.9
	Slack	1025	0	1137	0	1125	0
	Max. Flood	1400	2.3	1433	1.4	1345	2.0
Oct. 16	Slack	0310	0	0237	0	0250	0
	Max. Ebb	0610	1.2	0646	1.6	0600	2.5
	Slack	0920	0	1045	0	1015	0
	Max. Flood	1215	1.1	1240	0.5	1230	1.1
	Slack	1500	0	1436	0	1430	0
	Max. Ebb	1820	1.6	1904	2.0	1830	3.0
	Slack	2145	0	2316	0	2230	0
Oct. 17	Max. Flood	0045	1.4	0121	0.6	0040	1.4
	Slack	0345	0	0333	0	0310	0

The predictions based on the rule enunciated in the previous paper agree well with the observed currents in both time and velocity. It is believed that the error is well within the limits of accuracy of the data.

A comparison of sea level differences computed from the observed and predicted tides was made. It was found that differences as great as two feet occurred. These differences result in errors of as much as 0.4 knot in the calculated current. Such deviations from the predicted tides may be associated with weather in the vicinity, or in far distant parts of the ocean. In the present state of knowledge it appears necessary to accept these variations as normal in the prediction of the currents.

From this analysis it may be concluded that the present research is as reliable as the existing Current Tables, and considerably more informative concerning the currents through the whole of Juan de Fuca Strait.

Transport

The transport is the volume of water passing through a cross-sectional area in a limited time. This may be expressed as:

$$\text{Transport} = A\,\overline{V}\,T \qquad (2)$$

where A is the area of the cross-section of unit thickness, $\overline{V}$ is the average velocity during the time T.

An attempt has been made to calculate this transport through the cross-section (A, B, C) during the flood and ebb phases of an average tide cycle, and the net transport as the sum of these. The average tide cycle at Clayoquot and Point Atkinson was computed from the time and height data in the Tide Tables (1949). The average height of high and low water (705 tides) was determined and referred to mean sea level. The average duration of the falling tides was determined from the time data, and the average duration of the rise was assumed to be the difference between this and 745 minutes ($\pm$ 0.2 minute). The phase difference between the tides at Clayoquot and Point Atkinson was determined from the average time difference between corresponding high waters. With these data the average tide curves were plotted in the standard manner (Adams, 1947) as shown in Figure 7a.

From these curves the average difference of sea level was determined as shown in Figure 7b and from these values of ΔH, the average tidal velocity cycle at each observed depth (0, 15, 270 and 540 feet) was computed according to the rule (Herlinveaux, 1954) as shown in Figure 7c. The area under each arch of the velocity curves represented the product (VT) during the flood and ebb phases of the tidal flow. This quantity is the miles of water passing the point during the tidal phase and is conveniently designated as the tidal excursion. The flood and ebb excursions were plotted as functions of depth and interpreted by a smooth curve as shown in Figure 8a.

The net tidal excursion is the sum of the flood and ebb quantities as shown in Figure 8b. Here it was noted that there was an upper zone in which the ebb flow was dominant and a lower zone in which the flood was dominant. The depth

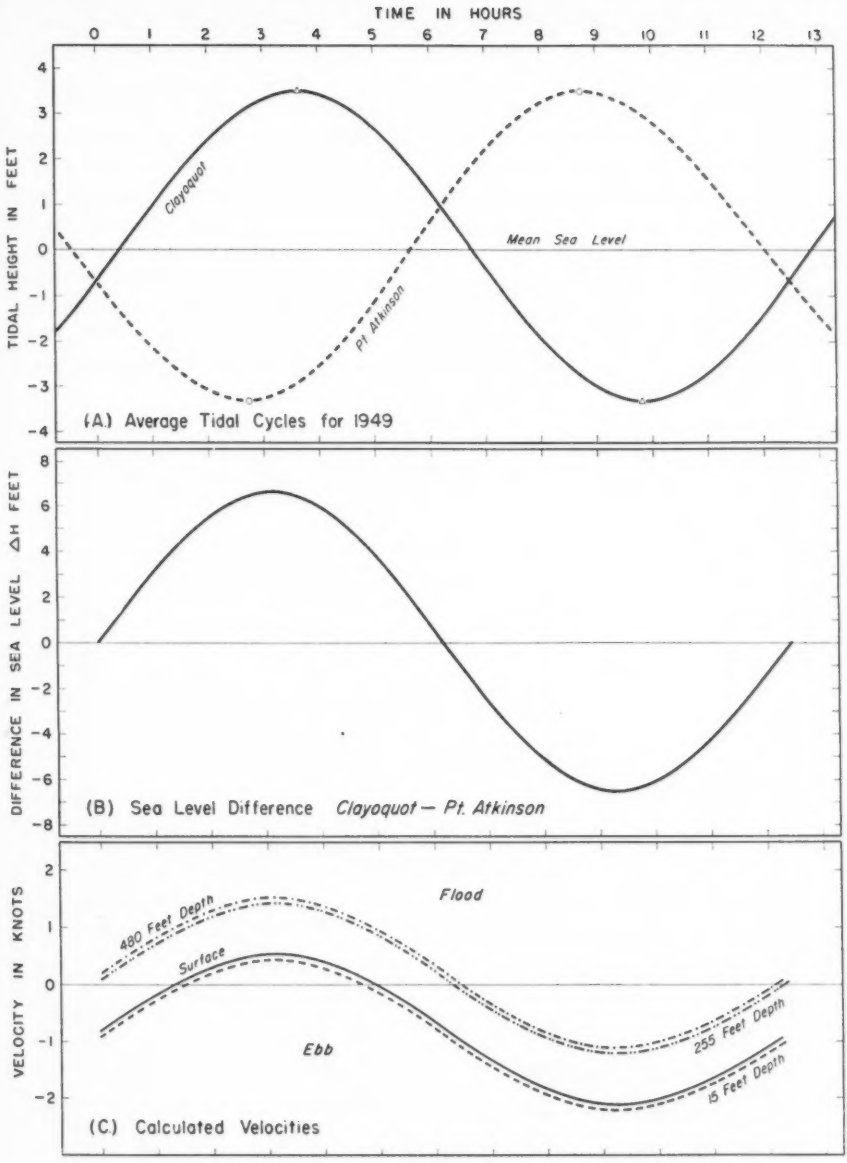
TIME IN HOURS
0 1 2 3 4 5 6 7 8 9 10 11 12 13
TIDAL HEIGHT IN FEET
4 3 2 1 0 -1 -2 -3 -4
Clayoquot
Pt. Atkinson
Mean Sea Level
(A) Average Tidal Cycles for 1949
DIFFERENCE IN SEA LEVEL ΔH FEET
8 6 4 2 0 -2 -4 -6 -8
(B) Sea Level Difference Clayoquot — Pt. Atkinson
VELOCITY IN KNOTS
2 1 0 -1 -2
Flood
480 Feet Depth
Surface
Ebb
255 Feet Depth
15 Feet Depth
(C) Calculated Velocities

FIGURE 7. Average tidal-height and current data, 1949.

(a) Average tide cycles, 1949 (Point Atkinson and Clayoquot).
(b) Cycle of sea level difference from Clayoquot to Point Atkinson.
(c) Average velocity cycles at observed depths at Station B.

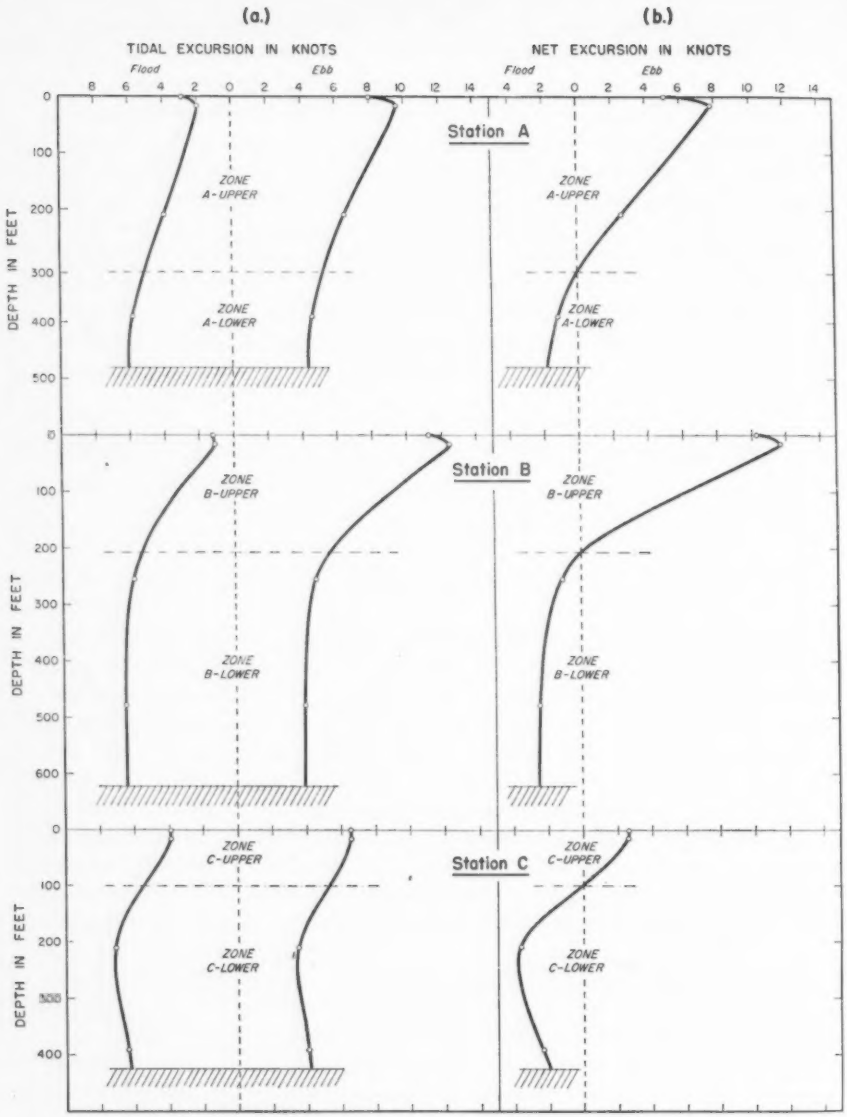

FIGURE 8. Tidal excursions during the average flood and ebb phases of the tide (1949) at Stations A, B, C, in Juan de Fuca Strait.

(a) Flood and ebb excursions, surface to bottom.
(b) Net excursions, surface to bottom.

of zero excursion was located as shown in Figure 8b. Then in Figure 8a the area between the curve and the zero ordinate in each zone, divided by the depth represents the average excursion at each station in each zone ($\overline{V}\,\overline{T}$).

The cross-section (A, B, C, Fig. 1) was arbitrarily divided into three segments (Fig. 9) in each of which the tidal velocity rule was assumed to be representative. The depths of zero excursion were noted and the boundary between the upper and lower zone interpreted by a smooth curve through these points. Then the area (A) of each section was determined graphically.

These values of excursion during flood and ebb flows and the areas of each of the six sections were set in Equation (2) and the individual transports were calculated as shown in Table IV. The Table also shows the net transport (the sum of the ebb and flood quantities) in each section, through the upper and lower zone, and through the whole strait.

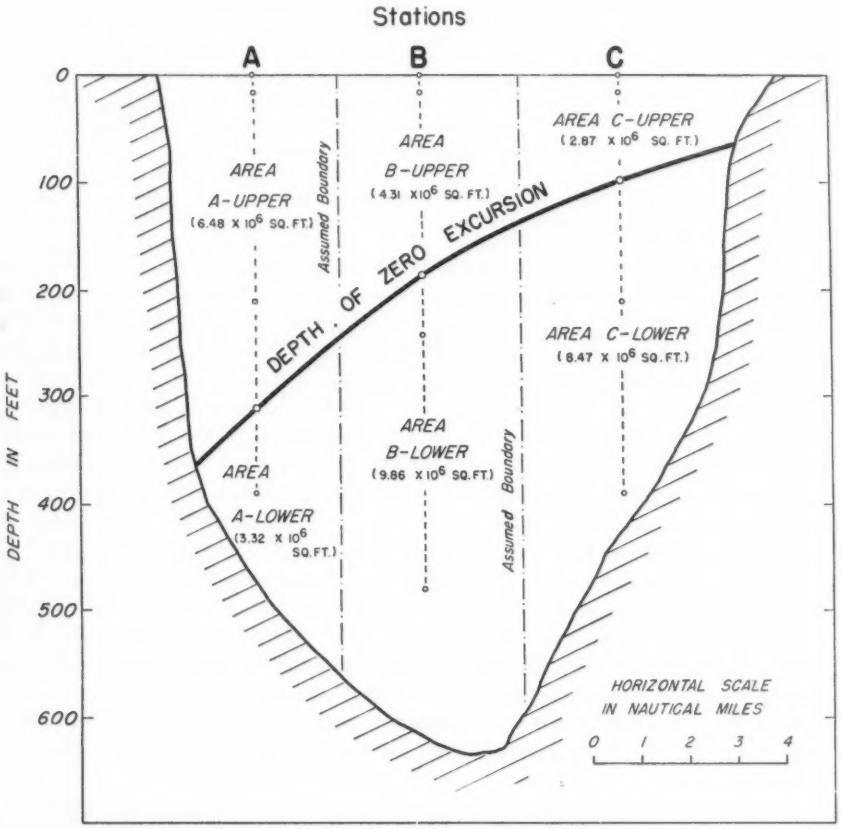

FIGURE 9. Cross-section A, B, C, where currents were observed in Juan de Fuca Strait. The depth of zero net excursion divides the cross-section into upper and lower zones.

TABLE IV. Calculated tidal transport through Juan de Fuca Strait for the average tidal cycle (745 minutes), 1949.

Upper zone: Transport $\times 10^{-10}$ cubic feet				
	A	B	C	Sum total transport
Flood	13.72	7.71	7.68	29.11
Ebb	29.57	25.04	10.76	65.37
Net transport	−15.85	−17.33	−3.08	−36.26

Lower zone: Transport $\times 10^{-10}$ cubic				
	A	B	C	Sum total transport
Flood	11.55	37.17	35.14	83.86
Ebb	9.59	26.12	20.51	56.22
Net transport	1.96	11.05	14.63	27.64

Net transport through whole cross-section, $\times 10^{-10}$ cubic feet

Flood	27.64
Ebb	−36.26
Resultant ebb transport	-8.62×10^{10} cubic feet

VALIDITY OF RESULTS

This analysis involves a sequence of three interpretations of data by smooth curves drawn through widely spaced points, each of which depends on integrals of the previous interpretation. The error in the average tide curves probably does not exceed 5%, but the error in the subsequent steps can be as great as 20% and may be cumulative. Evidently the estimate of transport is not likely to be better than a first-order approximation. Calculations were made from several different, but apparently reasonable, graphical interpretations and it was found that the net transport varied from 6 to 12×10^{10} cubic feet in the ebb direction.

There appears to be no doubt that the ebb is dominant in the upper zone, that the flood is dominant in the lower zone, and that the total ebb transport is greater than the flood. However, the quantitative estimate is in doubt.

It was shown by Tully (1953) that in such a system as this the total ebb discharge should exceed the flood inflow by the amount of land drainage during the tidal cycle. Georgia Strait has three outlets to the ocean. LaCroix and Tully (1954) have shown that the net transport through Seymour Narrows in the average tide cycle (1949) was 1.29×10^{10} cubic feet. The transport through Yuculta Rapids is not known but is probably small. Therefore, it may be assumed that the remaining land drainage finds its way to the ocean through Juan de Fuca Strait.

An estimate of the drainage was calculated. The average discharge of the Fraser River at Hope, B.C., is 91,000 cubic feet per second. From there to Georgia Strait the drainage basin is 4,500 square miles in which the discharge

increases on the average by about 36%. This is 7.8 cubic feet per second for each square mile. Assuming that this value is representative of the whole remaining coastal area draining into Georgia Strait and Puget Sound (30,630 square miles) this part of the runoff would be about 239,500 cubic feet per second, and the total land drainage would be about 365,500 c.f.s. Then in an average tide cycle (745 minutes—44,700 seconds) the volume would be 1.60×10^{10} cubic feet. Correcting this for the net transport through Seymour Narrows (1.29×10^{10} cubic feet) the net volume to be discharged through Juan the Fuca Strait would be of the order of 0.3×10^{10} cubic feet. According to this reasoning the net discharge should be almost zero and about one-tenth of that computed from the tidal data. Obviously this deduction is no better than that from the tidal data and cannot be regarded as disproof of the previous estimate. It is evident that a quantitative estimate of transport must await better data.

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Tisbe celata n. sp., a Harpacticoid Copepod from the Mantle Cavity of the Edible Mussel in New Brunswick[1]

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ABSTRACT

A new copepod, *Tisbe celata* (Harpacticoida: Tisbidae), is described from the mantle cavity of *Mytilus edulis* L. at St. Andrews, N.B., and its differentiation from the 27 known species of *Tisbe* is discussed.

INTRODUCTION

The genus *Tisbe* includes 27 valid species and several of doubtful standing. All are free-living, except *T. wilsoni* Seiwell 1928, which was described from *Amaroucium* at Woods Hole, Massachusetts. Two species, usually free-living, have been found associated with other animals. Gurney (1933) and Leigh-Sharpe (1935) recorded *T. elongata* (A. Scott, 1896) on the gills of *Homarus vulgaris* Milne-Edwards. Aurivillius (1885, 1887) found *T. furcata* (Baird, 1837) in *Molgula ampulloides* Van Beneden.

COLLECTION

During the first two weeks of August, 1953, 265 *Mytilus edulis* Linné were collected from the intertidal rocks, sandy gravel, and wharf piling in the immediate vicinity of the Atlantic Biological Station at St. Andrews, New Brunswick. The mantle cavities of 79 per cent of these mussels contained the new species of *Tisbe* to be described below. Each mussel had an average of two copepods, with the number found in a single mussel ranging from 1-41. Adults of both sexes and immature males were recovered. This copepod was not found in 203 *Mya arenaria* Linné taken from areas within a few feet of the *Mytilus*.

The mussels were opened separately in dishes of filtered sea water, the gills torn in shreds with needles, and the water stirred vigorously. The copepods swam fitfully and tended to return to fragments of the gills, so that frequent agitation was necessary to discover them in the debris. They were still vigorous eight hours after the mussels had been collected, provided the latter were stored without sea water in a cool place. If the mussels were kept without water at summer room temperatures, most of the copepods were dead at the end of the same period. If stored in sea water at room temperature, many copepods escaped from the mussels and were found dead on the bottom of the container.

DESCRIPTION

Tisbe celata n. sp.

The type material consists of 500 individuals representing both sexes from the mantle cavity of *Mytilus edulis* Linné at St. Andrews, New Brunswick,

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Canada. The holotype, allotype, and paratypes (150 females and 25 males) have been deposited in the United States National Museum. The remaining paratypes are in the author's collection.

FEMALE

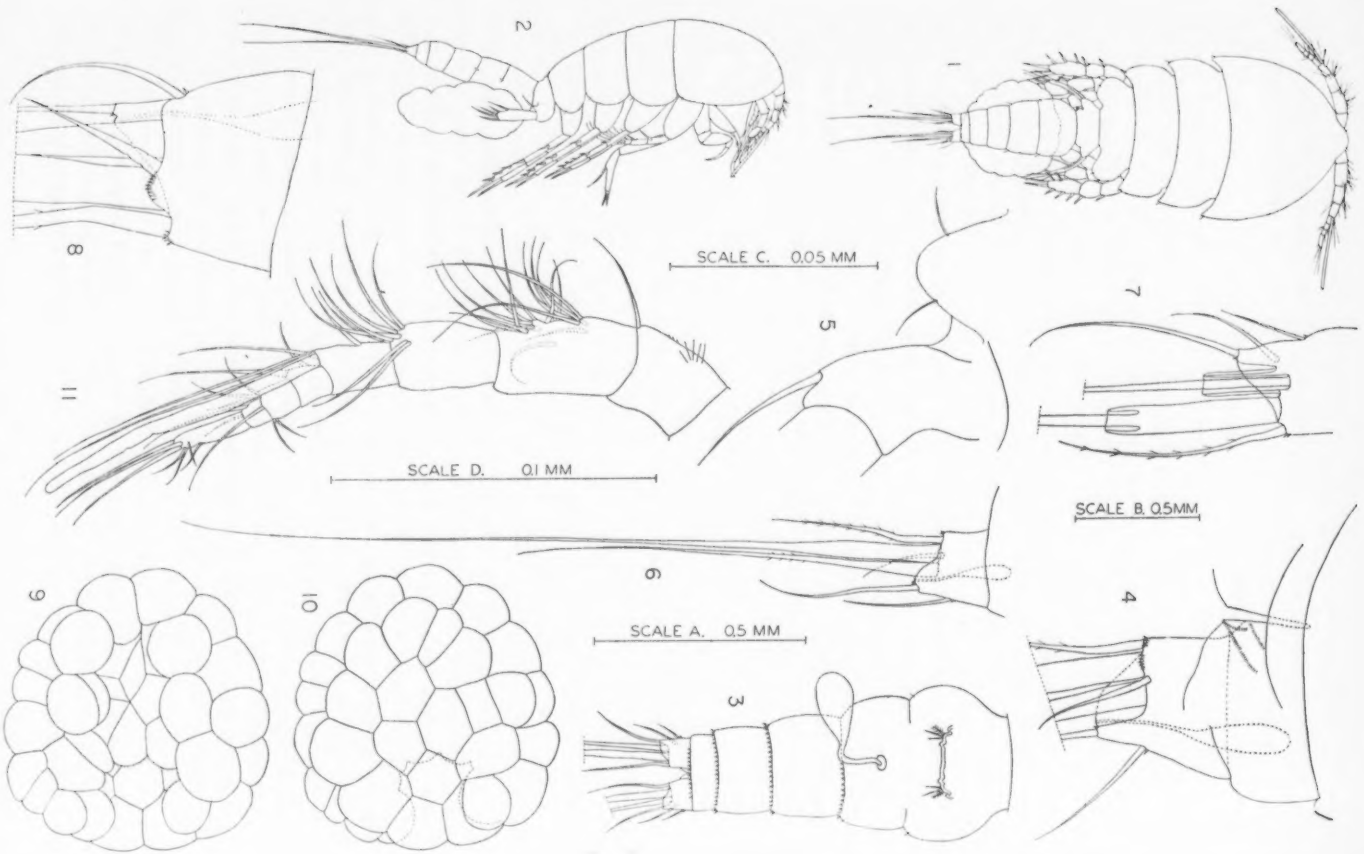
In living specimens the body is colorless, with the exception of a bright red eye and a white to pale orange egg sac. The body form (Fig. 1, 2) resembles that of other species in the genus. The total length (measuring from the tip of the rostrum to the posterior end of the caudal rami), based on five specimens, is 0.961 mm. (0.929-0.979 mm.). The greatest body width at the level of the first thoracic segment is 0.415 mm. The ratio of the length of the head (plus rostrum) and the first five leg-bearing segments to the genital segment and abdomen (plus caudal rami) is 2:1 (averaging 0.641 and 0.320 mm. respectively). The genital segment is distinctly divided dorsally and laterally by a transverse furrow. A minute slender seta about 10μ long is located near the posterior lateral margins of the first four thoracic segments and the genital segment, where there is an additional pair of these setae just in front of the transverse furrow. The abdomen (Fig. 3) is 3-segmented. The anal operculum is a smooth flap as shown in Figure 4. The actual and proportional lengths of the rostrum, body segments, and caudal rami are given in Table I.

TABLE I

Rostrum	Head plus somite of leg 1	2	3	4	5	6	1	2	3	Caudal rami
28μ	275	115	103	80	64	136	58	55	39	22
3	28	12	10	8	7	14	6	6	4	2 = 100

The rostrum (Fig. 5) is broadly rounded and bears the usual two minute setae. The genital and abdominal segments are armed along their posterior ventral margins with a row of minute spines (Fig. 3), but dorsally are unarmed. The caudal ramus (Fig. 6) is only slightly wider than long (29 $\times$ 25μ). The longest terminal seta measures 336μ in length. The innermost terminal seta is slightly bent near its base. The two long terminal setae may be partially retracted as shown in Figure 7. The short seta adjacent and external to the outer long seta is borne upon an expanded ventral corner of the ramus. The small dorsal seta has two weakly developed joints near its base (Fig. 8). All setae are naked except as indicated in Figure 6. An internal glandular sac which takes an intense stain with methylene blue opens near the base of the outermost terminal seta.

The egg sac (Fig. 9, 10) is dorsoventrally flattened and measures about 290 $\times$ 270μ, by 120μ in thickness, reaching to the bases of the caudal rami. In undissected whole mounts the egg sac appears slightly tapered posteriorly. The dorsal side, that is, the surface nearest the abdomen, is slightly concave, and the ventral side correspondingly convex. The egg sac contains about 45 eggs,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each about 54μ in diameter, though there is variation in egg size as indicated in the figures.

The first antenna (Fig. 11) has eight podomeres, with the actual and proportional lengths (measured along the anterior margin) as in Table II. The

TABLE II

1	2	3	4	5	6	7	8	
38μ	60	44	27	15	14	10	28	
16	26	19	11	6	6	4	12	= 100

TABLE III

	Endopodite						Average		Exopodite						Average	
1st podomere	75	91	61	85	91	88	87	82	49	49	35	45	49	45	47	45
2nd podomere	59	98	32	96	94	95	95	81	36	53	30	50	56	47	46	45
3rd podomere	6	7	10	8	7	8	7	7.5	22	20	13	23	19	21	20	20
Total	140	196	103	189	192	191	189	171	107	122	78	118	124	113	113	110

entire antenna exclusive of setae is about 236μ in length. On the fourth podomere there is an aesthetask 125μ long, extending well beyond the tip of the antenna. The second antenna (Fig. 12) is of the usual form in the genus, with the four podomeres of the endopodite somewhat indistinctly separated.

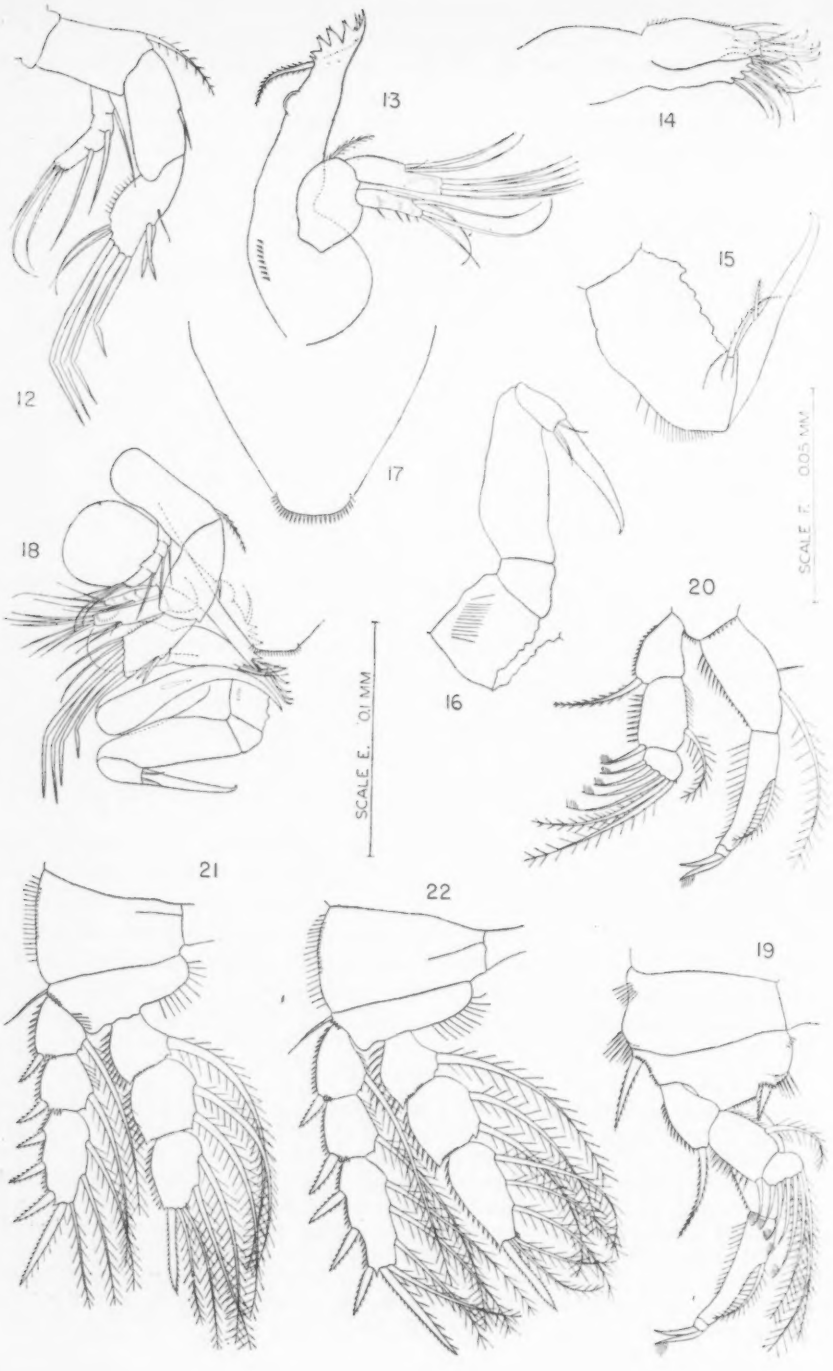
The mandible (Fig. 13), first maxilla (Fig. 14), second maxilla (Fig. 15), and maxilliped (Fig. 16) are of the usual form in the genus. The labrum (Fig. 17) is triangular and truncated at the posterior ventral apex where it bears a row of slender spines. The relative position of the mouth parts is shown in Figure 18.

The exopodite of the first pair of swimming legs (Fig. 19) is shorter than the endopodite, and, in the usual position assumed in specimens preserved in 70 per cent ethyl alcohol, bent at an angle so as to cross behind the endopodite. The average length of the endopodite podomeres (based on seven mature females) are 82, 81 and 7.5μ, respectively. The expodite podomeres measure 45, 45 and 20μ. The relative and absolute lengths of the podomeres vary considerably, so that in some individuals the second endopodite podomere may be longer than

PLATE I (FIG. 1–11)

(All figures were drawn with the aid of a camera lucida. Scale A applies to Fig.1 and 2; scale B to Fig.3, 9, 10, 19–23 and 26; scale C to Fig.4, 29 and 31; scale D to Fig.5, 7 and 32; scale E to Fig.6, 11–17, 24, 27, 28 and 30; scale F to Fig.8 and 25; and scale G to Fig.18.)

Tisbe celata, adult female. **1.** Dorsal view **2.** Lateral view. **3.** Genital segment and abdomen, ventral view, showing spermatophore attached. **4.** Caudal ramus and last abdominal segment with operculum, dorsal view. **5.** Rostrum and first antennal podomere, dorsal view. **6.** Caudal ramus, ventral view. **7.** Caudal ramus, ventral view, to show partly retracted setae. **8.** Caudal ramus, dorsal view. **9.** Egg sac, dorsal view, showing the concave surface next to the abdomen, drawn under slight pressure. The stippling indicates the concavity at the point of attachment. **10.** Same egg sac, ventral view. **11.** First antenna.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the first and in others shorter. In view of the importance placed upon this relationship as a specific character, the measurements in microns of seven females are given in Table III.

The two rami are shown separated in Figure 20. The basipodite bears a stout spine on the outer and inner corners.

The second (Fig. 21), third (Fig. 22) and fourth (Fig. 23) pairs of swimming legs are similar except for certain differences in armature, as indicated below, and in the proportions of the podomeres. The strong inner basipodite spine is absent on all three pairs, and the outer basipodite spine is more slender. Table IV gives the spine and setal formula for the first four pairs of legs.

TABLE IV

	Leg 1		Leg 2		Leg 3		Leg 4	
	Exp.	End.	Exp.	End.	Exp.	End.	Exp.	End.
1st podomere	1:0	0:1	1:1	0:1	1:1	0:1	1:1	0:1
2nd podomere	1:1	0:1	1:1	0:2	1:1	0:2	1:1	0:2
3rd podomere	6	2	7	5	8	6	8	5

The proximal podomere of the fifth leg (Fig. 24) bears three slender setae on the inner expansion, the middle seta long (115μ) and the other two shorter but subequal (48μ). There is a single seta (44μ) at the outer corner of the podomere. Four internal glandular sacs which take an intense stain with methylene blue open on or near the inner edge of the inner expansion as shown in the Figure. The distal podomere is 3.1 times longer than wide, with the average of 14 specimens being 97 $\times$ 31μ. There are four terminal setae, three subequal in length (46-51μ) and the next to the innermost of the quartette much longer (67μ). A fifth seta is located on the outer edge of the podomere at the junction of the distal two quarters (73μ from the base). Small spines occur along both edges of the podomere. The slightly convex outer broad surface of the podomere has a few small spines as indicated in the Figure. An internal glandular sac which may be colored intensely with methylene blue opens at the inner distal corner of the podomere. The sixth pair of legs (Fig. 25), visible on the ventral anterior part of the genital segment, is represented by three setae on either side of the opening of the oviduct.

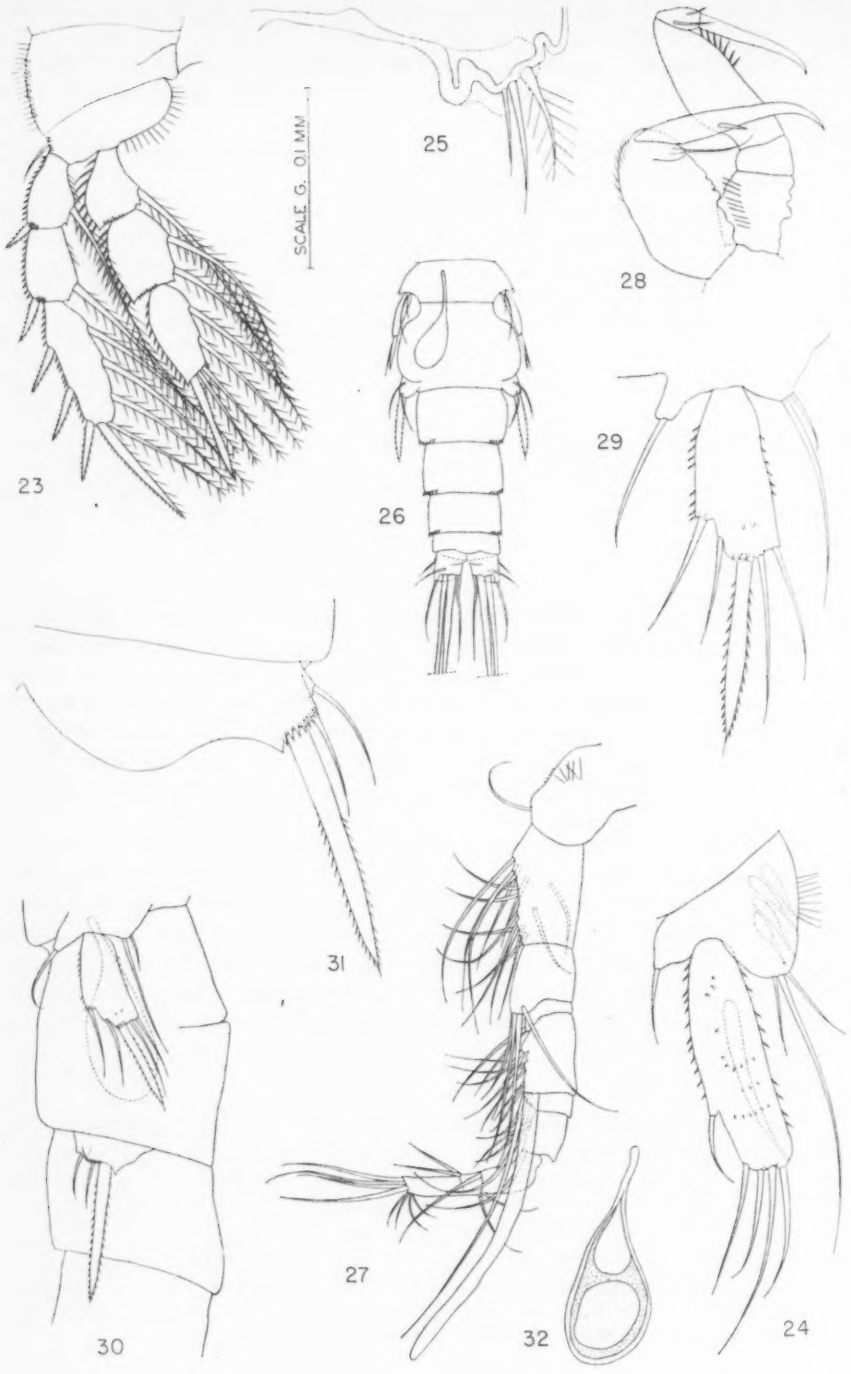
MALE

The color and body form resemble the female. The total length (measured as in the female and based on five specimens) is 0.781 mm. (0.765-0.800 mm.).

PLATE II (FIG. 12–22)

(See Plate I caption for scale.)

Tisbe celata, adult female. **12.** Second antenna. **13.** Mandible. **14.** First maxilla. **15.** Second maxilla. **16.** Maxilliped. **17.** Labrum. **18.** Second antenna, labrum, and mouth parts in position, ventral view. **19.** First leg, with rami in position assumed in alcoholic specimens. **20.** Rami of first leg separated. **21.** Second leg. **22.** Third leg.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The greatest body width is 0.328 mm. at the level of the first thoracic segment. The ratio of the length of the head (plus rostrum) and the first five leg-bearing segments to the genital segment and abdomen (plus caudal rami) is 2.17:1 (averaging 0.543 and 0.250 mm., respectively). The abdomen (Fig. 26) is 4-segmented. Table I gives the actual and proportional lengths of the rostrum, body segments and caudal rami.

TABLE V

Rostrum	Head plus somite of leg 1	2	3	4	5	6	1	2	3	4	Caudal rami
25μ	223	70	83	64	57	61	58	51	38	19	20
3	30	9	10	8	7	8	7	7	5	3	3 = 100

The caudal ramus is like that of the female. The first antenna (Fig. 27) is subprehensile and has nine podomeres, the third apparently subdivided into two, so that the proximal part of the antenna comprises five podomeres and the distal part four. The actual and proportional lengths of the podomeres are as in Table

TABLE VI

1	2	3	4	5	6	7	8	9
30μ	48	23	6	29	9	21	22	32
13	22	11	3	13	4	10	10	14 = 100

VI. The entire antenna is about 220μ in length, and the aesthetask on the fifth podomere measures 109μ in length. The second antenna and mouth parts are like those in the female, except for the maxilliped (Fig. 28) which has a row of spines along the distal inner edge of the longest podomere.

The first, second, third and fourth swimming legs are like those of the female, and have the same spine and setal formula.

The distal podomere of the fifth pair of legs (Fig. 29, 30) is shorter than in the female, with a ratio of length to width of 2.4:1, the average dimensions of four males being 42 $\times$ 18μ. A few minute spines may be seen on the slightly convex broad outer surface. The middle spine (43μ) is broad and attenuated to

PLATE III (FIG. 23–32)

(See Plate I caption for scale.)

Tisbe celata, adult female. **23.** Fourth leg. **24.** Fifth leg. **25.** Sixth leg.

Tisbe celata, adult male. **26.** Genital segment and abdomen, dorsal view. **27.** First antenna. **28.** Second maxilla and maxilliped. **29.** Fifth leg. **30.** Fifth and sixth legs in position, lateral view. **31.** Sixth leg, lateroventral view. **32.** Spermatophore.

a fine hair-like tip. The inner expansion of the proximal podomere is less pronounced than in the female and bears two setae, one long (57μ) and one short (17μ). The sixth pair of legs (Fig. 30, 31) consists of a broad lobe bearing a spinose, broad, distally attenuated seta about 57 $\times$ 5.5μ and two outer short, slender, naked setae, the outermost on a low projection. There is a row of small spines near the bases of the two inner setae. The spermatophore (Fig. 32) measures 70 $\times$ 30μ including the slender neck.

DISCUSSION

Comparative study of the species in the genus *Tisbe* is made difficult because of the often incomplete original descriptions. *T. celata* may be separated, however, however, from the several already known species as follows:

1. Distal podomere of the fifth leg in the female four or more times longer than wide
T. cluthae (T. Scott, 1899), *elegantula* (Sars, 1905), *ensifer* Fischer 1860, *gracilis* (T. Scott, 1895), *graciloides* (Sars, 1920), *gurneyi* (Lang, 1934), *longicornis* (T. Scott, 1895), *longisetosa* Gurney 1927, *remota* (Farran, 1926), and *tenera* (Sars, 1905)

Distal podomere of the fifth leg of the female only two or less times longer than wide
T. angusta (Sars, 1905), *austrina* T. Scott, 1912, *elongata* (A. Scott, 1896), and *tenella* (Sars, 1910)

Distal podomere of the fifth leg of the female between two and four times longer than wide 2

2. First antenna of the female with the second and third podomeres of equal length
T. dilatata Klie, 1949, *finmarchica* (Sars, 1905), *minor* (T. Scott and A. Scott, 1896), and *tenuimana* (Giesbrecht, 1902)

First antenna of the female with the third podomere longer than the second
T. bermudensis Willey 1930

First antenna of the female with the second podomere longer than the third 3

3. Second podomere of the endopodite of the first leg of the female distinctly longer (1½ times) than the first *T. gracilipes* T. Scott, 1912

Second podomere of the endopodite of the first leg of the female distinctly shorter (0.8–0.5 times) than the first
T. compacta (Sars, 1920) and *racovitzai* (Giesbrecht, 1902)

Second podomere of the endopodite of the first leg of the female about equal to or only slightly longer than the first 4

4. Outermost seta on the distal podomere of the fifth leg in the female separated from the nearest seta by 0.18 or less of the distance between the latter seta and the base of the podomere *T. furcata* (Baird, 1837), *inflata* (Sars, 1909), *reticulata* Bocquet, 1951, and *varians* T. Scott, 1914

Outermost seta on the distal podomere of the fifth leg in the female separated from the nearest seta by 0.26 or more of the distance between the latter seta and the base of the podomere 5

5. Distal podomere of the fifth leg in the female 2.6 times longer than wide, with the outermost seta separated from the nearest seta by 0.31 of the distance between the latter seta and the base of the podomere. Apical setae on the third podomere of the endopodite of the first leg of the female without plumes *T. wilsoni* Seiwell 1928

Distal podomere of the fifth leg in the female 3.1 times longer than wide, with the outermost seta separated from the nearest seta by 0.26 of the distance between the latter seta and the base of the podomere. Inner apical seta of the endopodite of the first leg of the female penicillate *T. celata* mihi

The new species differs further from *T. furcata*, a common and apparently closely related species, in having the inner of the two long terminal setae on the caudal ramus entirely naked, in the distal podomere of the fifth leg in the female being 3.1 times longer than wide instead of 3.5, in having the outermost seta on the distal podomere of the fifth leg of the female separated from the nearest seta by 0.26 of the distance between the latter and the base of the podomere instead of 0.11, in the basal expansion of the fifth leg in the male having two setae instead of one, in the distal podomere of the fifth leg of the male being 2.4 times longer than the wide instead of 3.0, in the body being colorless instead of being more or less distinctly banded transversely with clear crimson, and in the egg sac extending only to the beginning of the caudal rami instead of well posterior to the end of the rami.

T. celata would seem to be a parasite of *Mytilus edulis* rather than a free-swimming species accidentally introduced into the mantle cavity, since it occurs only in that mussel and then in relatively large numbers, and since the presence of immature stages indicates that it probably breeds in the mussel.

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Growth, Maturity and Mortality in the Relatively Unexploited Lake Trout, *Cristivomer namaycush*, of Great Slave Lake[1]

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ABSTRACT

Ages of 9,215 lake trout were determined. Length-weight and time-maturity relationships are shown. Sex ratio is 1:1. Only half the females of mature size spawn each year. There is no growth except during June to September, inclusive. There is a tremendous difference in size at a given age. Growth is much faster in one half of the lake than in the other, it is the same as or slightly slower than in lakes farther south and considerably faster than in Great Bear Lake. Seven years of commercial fishing did not increase total annual mortality by much. Mortality rate increases with age among all fish of catchable size. A given year-class probably attains maximum biomass well before most of its members reach commercial size. No significant variation in year-class strength was found.

INTRODUCTION

Until 1945 Great Slave Lake had never been exploited except for an insignificant fishery for local use. Following preliminary exploration by Dr. D. S. Rawson under the auspices of the Fisheries Research Board of Canada and on his recommendation, commercial fishing began late in the fishing season of 1945 and has continued until the present time. Lake trout, *Cristivomer namaycush*, and lake whitefish, *Coregonus clupeaformis*, constitute 95 per cent of the commercial catch, the other commercial species being inconnu, *Stenodus leucichthys mackenziei*, northern pike, *Esox lucius*, and yellow walleye, *Stizostedion vitreum vitreum*.

In 1946, as directed by the Fisheries Research Board of Canada, the author initiated a study of the new commercial fishery which included collecting scale samples of whitefish and lake trout for age determinations. The results for whitefish have been published (Kennedy, 1953). This paper reports similar results based on scale samples and related data for the trout collected to date.

Great Slave Lake is the fifth largest lake in North America, being smaller than Superior, Huron, Michigan and Great Bear. On the basis of the most recently published aerial survey maps its area is calculated to be 11,070 square miles, of which 10,430 square miles are water and the remainder islands. Rawson (1950, 1951, 1953) has thoroughly described the general nature of the lake, its limnology and its fauna.

ACKNOWLEDGMENTS

It is with pleasure that the author acknowledges assistance from the twenty or more members of field parties who at various times collected scale samples.

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The painstaking work of Miss L. D. Brown in making the age determinations is greatly appreciated.

MATERIALS AND METHODS

Most of the scales used for age determinations were taken from fish caught by commercial fishermen and are referred to here as commercial fish. For this purpose the seven scale-sampling stations whose positions are indicated on Figure 1 were established, each embracing an area ten miles in diameter. The station numbers are roughly in order from southwest to northwest, that is, from the moderately oligotrophic to the extremely oligotrophic parts of the lake. Ideally, subsamples totalling about 500 fish each year were taken at random from all the fish caught by commercial fishermen in the sampling area. However, in earlier years the samples were often considerably smaller than the ideal 500, and in 1946 and 1947 some of the subsamples (6½ per cent of all the scales taken) were even outside the defined area of the scale-sampling station which they were presumed to represent. All commercial fish were caught in gill-nets of 5½-inch mesh (stretched measure), the major part of them in 30/6 cotton web, but an appreciable part, particularly at Stations I, II and III, of finer cotton or nylon web.

From each fish in the sample several scales were taken from the region midway between the dorsal fin and the lateral line. They were placed in a coin envelope on which was recorded date and place of capture and the weight. It was not practical to examine the gonads of commercial fish.

Scales were also taken from some of the trout caught in the standard gangs fished by Dr. Rawson's field parties and by the author—they are called standard-gang fish as opposed to commercial fish. A standard gang of gill-nets, as described by Rawson (1951), consists of 50 yards each of 1½-inch, 2-inch, 3-inch, 4-inch, 5-inch and 5½-inch mesh (stretched measure). Sometimes Dr. Rawson's field parties tended to take scales from a disproportionate number of the smallest and of the largest fish, so in some respects they cannot be considered as a random sample of all the trout caught in standard gangs. They took trout at various places scattered over the whole lake in 1944, 1945 and 1946 (mostly 1946), while the author took them only in the vicinity of Gros Cap in 1946. Scale samples were taken from standard-gang fish in exactly the same way as from commercial fish except that in most cases the length (from the tip of the snout to the distal end of the shortest caudal ray) and data based on observations of the gonads were also recorded.

All scale samples were examined later in the laboratory to determine age. For each sample a few scales were removed from the envelope, cleaned if necessary, and mounted temporarily in water between two glass slides. The mounted scales were magnified about 60 diameters by means of a projector, and the number of annuli were counted. Much preliminary work was done on developing techniques including reading scales which had already been read by investigators in Saskatchewan and Ontario. It was found that, with practice, the annuli could be easily distinguished on most scales. Only breaks in the pattern which could

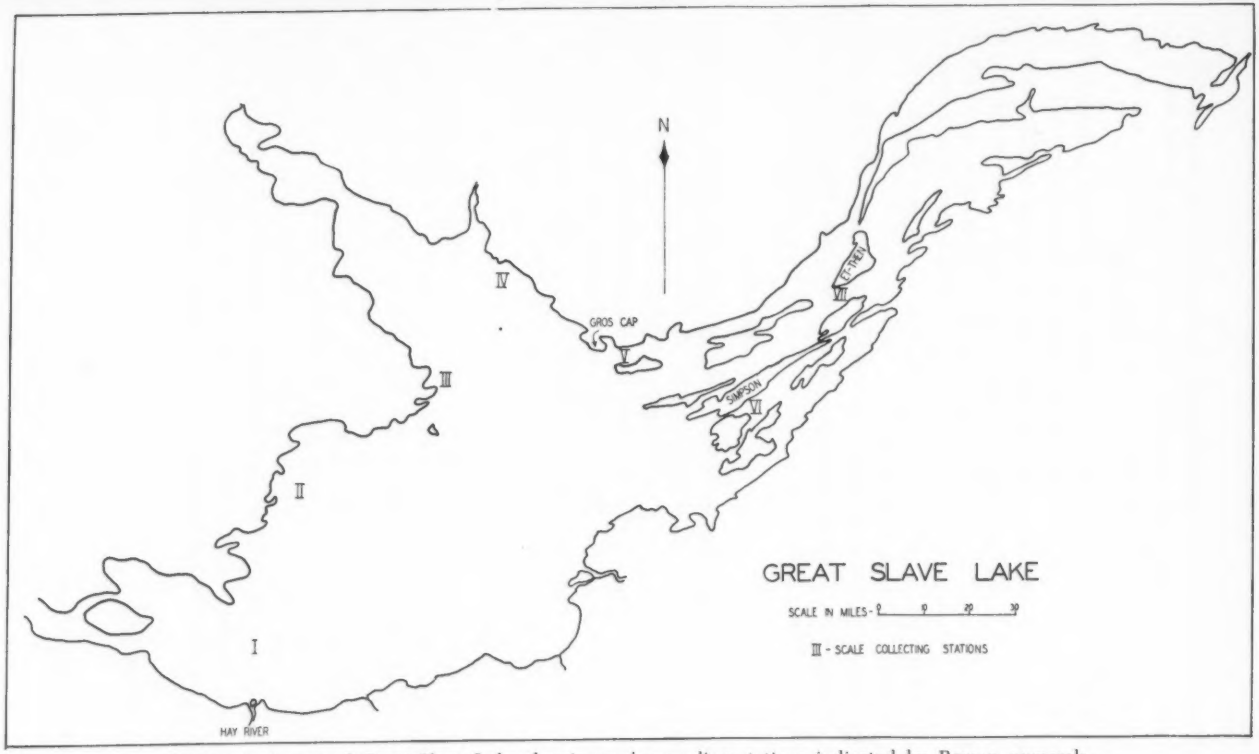

FIGURE 1. A map of Great Slave Lake showing scale-sampling stations indicated by Roman numerals.

be followed completely around the scale were regarded as true annuli, and all such were so regarded. All age determinations were made by one technician who, under the author's supervision, made decisions regarding age on the basis of the examination of at least two scales from each fish.

For about 15 per cent of the sample there was difficulty in deciding whether or not to consider certain markings as annuli. However, the scale reader was required to make some decision regarding age, on the grounds that disregarding difficult scales would probably bias the results more than incorrect readings. For this reason certain individual readings may be in error, generally by one year, occasionally by more, but it is the author's opinion that there is approximately an equal chance of any error being positive or negative so that averages based on the readings are essentially correct.

Ages were assigned to 8,671 commercial trout and to 544 standard-gang trout. All were caught over the period 1944 to 1952, the period under consideration in this paper.

GENERAL INFORMATION

It would be preferable to have more data on the length-weight relationship, on time of maturity, on sex ratio, and on the frequency of spawning of Great Slave Lake trout than has been collected. However, since it is unlikely that such will be available in the near future it seems advisable to make a summary of the data on hand. The data are regarded as inadequate to justify publishing a more detailed treatment than that given below. A more detailed analysis is on file at the Central Fisheries Research Station of the Fisheries Research Board.

The Length-Weight Relationship

Although the size of commercial trout was always recorded in terms of weight only, both length and weight were determined for most standard-gang trout. The standard-gang samples are regarded as representative enough of all Great Lake trout in this respect that the data can be used to indicate the general length-weight relationship. To determine this relationship the average weight and length at each age was calculated, and the respective logarithms were plotted graphically (not shown). All the points representing mature trout fell on or close to one straight line, and all the points representing immature fish fell on or close to another straight line. The respective straight lines were fitted by inspection, and from their equations length-weight relationships were calculated as:

for immature fish

$$y = 0.000238x^{3.16}$$

and for mature fish

$$y = 0.000413x^{3.02}$$

where y is the weight in pounds and x is the fork length in inches.

The relationship between average length and average weight is also shown in Table I.

TABLE I. The relationship between average fork length in inches and average weight in pounds derived from a representative sample of Great Slave Lake trout.

Length	Weight	Length	Weight	Length	Weight	Length	Weight
inches	*lb.*	*inches*	*lb.*	*inches*	*lb.*	*inches*	*lb.*
7	0.11	16	1.52	25	6.19	34	15.4
8	0.15	17	1.84	26	7.22	35	16.6
9	0.25	18	2.30	27	8.10	36	18.0
10	0.35	19	2.95	28	8.90	37	19.5
11	0.47	20	3.40	29	9.90	38	21.2
12	0.62	21	3.88	30	10.8	39	22.6
13	0.80	22	4.43	31	11.8	40	24.4
14	1.00	23	5.02	32	13.0	41	26.2
15	1.24	24	5.65	33	14.2	42	27.7

There was no apparent difference between males and females in their length-weight relationship either when mature or when immature.

MATURITY

The state of maturity was recorded for the standard-gang fish collected by the author at Gros Cap in 1946. All were recorded as mature, on the basis of a gross examination, if in the examiner's opinion (generally the author, occasionally scientific personnel under his supervision) the appearance of the gonad indicated that the fish had ever spawned or that it would likely have spawned during the current year. All other fish were recorded as immature.

The ratio of immature fish was determined at each age—the ratios were approximately the same for each sex. These ratios were plotted graphically against age, and a freehand curve was drawn which fitted the points reasonably well. From the curve (not shown) the average at which certain proportions of the sample would be mature were read off and recorded in Table II. The relationships shown in Table II between proportion mature and size were determined in a comparable manner.

In addition to the 346 trout (116 immature, 180 mature), used in the above analysis, four males were disregarded. One case of maturity at a considerably smaller size than was consistent with the remaining data was regarded as being the result of incorrect recording. Three cases of immaturity in males at a con-

TABLE II. The progress of maturity in Great Slave Lake Trout, derived from a representative sample.

	Year of life	Length[a]	Weight[a]
		inches	*lb.*
None mature until	5th	15.0	1.4
25% mature when in	7th	17.8	2.4
50% mature when in	8th	18.4	2.7
75% mature when in	9th	19.5	3.2
All mature by	11th	23.0	5.0

[a]Size approximately halfway through the growing season.

siderably larger size than was consistent with the remaining data were regarded as probably mature fish which were not spawning during the current year (cf. below.).

The earliest maturing fish tended to be those which were largest for the age. Mature fish averaged about 10 to 15 per cent heavier at a given length than immature fish. This latter fact accounts for the seeming discrepancy between the length-weight relationship indicated by Table II, as compared with Table I.

Since the samples were taken randomly (in so far as it is ever possible to take a random sample of fish by gill-nets), and since Gros Cap is centrally located, the results are presumed to apply to Great Slave Lake trout in general.

Sex Ratio

Sex was recorded for 412 standard-gang trout taken at various places and can be regarded as a representative sample in this respect. Of this number 207 were males and 205 were females. The sex ratio of Great Slave Lake trout can therefore be regarded as approximately 1:1.

Frequency of Spawning

Some mature fish of various species in northern lakes spawn less often than once per year. Several cases are cited by Kennedy (1953), including cases specifically involving lake trout. Great Slave Lake trout apparently are one of the populations in which mature individuals do not spawn every year.

The mature female trout from standard gangs, which the author examined at Gros Cap in 1946, could be readily divided into two groups on the basis of the appearance of the ovary. In the one group, ovaries contained eggs which were practically as large as those produced at spawning times. Fish in this group were recorded as "large eggs" and it was obvious that they would have spawned later in the year had they not been captured. In the other group the largest eggs were considerably smaller and the whole ovary was intermediate in size between an immature female and a "large eggs" female, in fact it might have been mistaken by the unwary for an immature ovary. However, there were generally the remains of a few fully developed eggs obviously retained from some previous spawning, and any case the ovary was ruptured in the characteristic way of all trout that have spawned. The latter group were recorded as "small eggs" and it was obvious that they were fish that had spawned and probably would have spawned again, but not in the current year, had they not been captured.

Of those records which can be regarded as constituting a strictly representative sample, there were 49 cases recorded as "small eggs", 54 cases recorded as "large eggs". This is not appreciably different from a 1:1 ratio between the two conditions. Rough observations on trout from various parts of the lake indicated approximately the same ratio everywhere between "large eggs" and "small eggs" and observations made during other years indicate that 1946 was not an atypical year in this respect.

It therefore appears that only about one-half of the mature female Great

Slave Lake trout spawn in any given year, that is, that the average female spawns about every other year.

Whether or not the corresponding males spawn annually could not be determined from a gross examination of the gonads. However, the testes do vary greatly in size and, as is suggested above under "maturity", may even be small enough to be mistaken for immature testes. This indicates that probably at least some of them do not spawn every year.

SEASONAL GROWTH

The outer parts of all scales taken from Great Slave Lake commercial trout caught any time between September and the following June look much the same. Starting in late June some scales show an annulus at the very edge. In successively later samples more and more of them show annuli. The area outside each new annulus increases until September when the appearance is again much the same as it was in early June, (i.e. the area outside the last annulus is almost as wide as is the area between the outer annulus and the one next inside it). Obviously the progression represents annulus formation followed by seasonal growth in scale diameter. On the basis of general knowledge of the relationship between fish and scale size, it can also be regarded as approximately representing seasonal growth of the whole fish. On this basis trout begin to increase in size (including weight) some time after the middle of June (the day of commencement of growth varies considerably from fish to fish), and continue only until September, after which there is no further growth until the following June.

This seasonal growth was measured using the same techniques as outlined elsewhere (Kennedy, 1953, p. 420), with the exception that the measurements were taken along an antero-lateral ridge (either one) instead of along the dorso-ventral diameter. On each scale sample used for this purpose the following distances were measured: from the outside of the outermost annulus, "AB"; from the outermost annulus to the one next inside it, "BC"; from that annulus to the one inside it, "CD"; and from that annulus (third from the edge) to the one inside (fourth from the edge), "DE". Representative samples, each consisting of the scales from 20 or more commercial trout, were measured in this way and the average of each of the distances was determined for each sample. The ratio AB/BC (based on average AB's and BC's) was calculated for each sample. Values for this ratio at different places and on all dates more than six days apart are given in Table II. Obviously AB/BC represents growth until the date of capture compared with growth for the previous year.

The ratios BC/CD and CD/DE were also calculated for each sample. These ratios represent, respectively, growth "last year" compared with growth "two years ago", and growth "two years ago" compared with growth "three years ago". After a preliminary examination has shown that these respective ratios tended to have a normal distribution around a mean, and that the sampling station or calendar year did not greatly influence departure from the mean, the average values for the ratios were calculated. They were found to be 84.8 per cent for BC/CD and 90.9 per cent for CD/DE. These ratios differ because the

TABLE III. The ratio of growth until time of capture to total growth during the previous year (i.e., AB/BC) also the proportion of fish in the sample which show growth since May 1 of the year of capture in representative samples of Great Slave Lake commercial trout taken at the indicated times and places.

Station	Date	Av. ratio AB/BC	Fish showing growth	Station	Date	Av. ratio AB/BC	Fish showing growth
		%	%			%	%
I	Jan. 4/49	77	100	IV	July 14/47	57	100
I	Jan. 15/49	70	100	IV	July 18/50	53	100
I	Feb. 3/49	70	100	IV	Aug. 13/47	47	100
I	Feb. 13/49	73	100	IV	Aug. 27/47	68	100
I	Mar. 2/49	67	100	IV	Aug. 29/49	67	100
I	June 29/49	47	100	IV	Aug. 29/50	73	100
I	July 5/49	26	80	IV	Aug. 30/52	72	100
I	Sept. 4/52	73	100	IV	Sept. 4/49	77	100
I	Dec. 30/49	77	100	V	July 8/47	14	40
II	July 18/50	63	100	V	July 31/47	53	100
II	July 24/49	62	100	V	Aug. 6/47	33	85
II	July 30/49	58	100	V	Aug. 8/50	61	100
II	July 31/50	52	100	V	Aug. 13/47	58	100
II	Aug. 16/49	63	100	V	Aug. 20/47	55	100
III	June 25/51	8	25	VI	July 15/49	66	100
III	June 29/50	49	100	VI	July 21/49	67	100
III	July 9/52	2	5	VI	Aug. 7/49	66	100
III	July 11/47	24	100	VI	Aug. 17/50	61	100
III	July 11/49	61	100	VI	Aug. 22/52	59	100
III	July 12/46	39	100	VI	Aug. 25/50	74	100
III	July 14/50	52	100	VII	July 21/52	51	100
III	July 20/46	58	100	VII	July 27/50	59	100
III	July 22/49	57	100	VII	Aug. 3/50	69	100
III	Aug. 19/52	52	100	VII	Aug. 16/49	67	100
III	Aug. 28/52	67	100	VII	Aug. 24/47	58	100
IV	July 1/46	42	100	VII	Aug. 28/49	63	100
IV	July 7/52	15	45	VII	Sept. 2/49	76	100

average growth made each year is appreciably less than that made the year before, that is, AB/BC can never be as great as 100 per cent. The average of the six values which represent winter months is 72.25 per cent which can be regarded as one estimate of the maximum possible value for AB/BC. Another estimate can be made on the assumption that AB/BC is as much less than BC/CD as BC/CD is less than CD/DE. Since BC/CD is 93.3 per cent of CD/DE, the maximum possible value of AB/BC could be regarded as 93.3 per cent of BC/CD that is $93.3 \times 84.8 = 79.1$ per cent. The value 75 per cent is a convenient compromise between the two estimates and it is assumed in this paper that the scales of typical Great Slave Lake commercial trout increase in radius each year by only about 75 per cent of the previous year's increment.

On this assumption, if each of the values for AB/BC given in Table III is divided by the factor 0.75, it would give a value which would represent the average proportion of the potential annual growth which each fish had made by the date of capture. Values calculated in this way are plotted in Figure 2. A freehand curve is drawn among them to represent the best available estimate of seasonal growth of Great Slave Lake commercial trout.

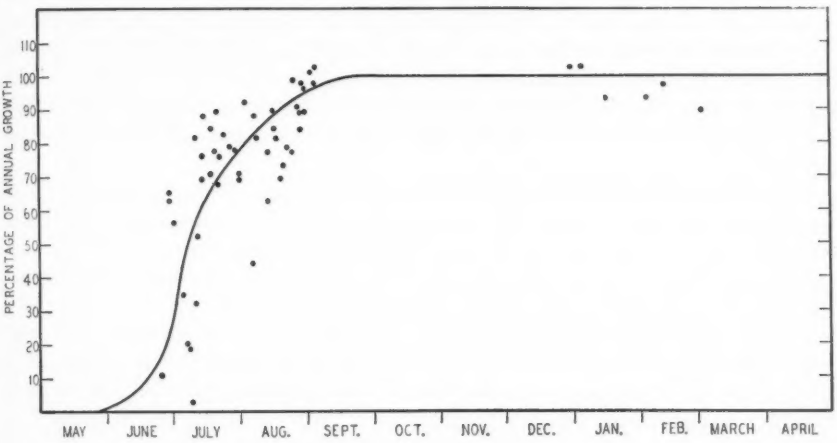

FIGURE 2. Seasonal growth as shown by samples of Great Slave Lake trout captured at various times, where the amount of scale growth made to the date of capture is expressed as a percentage of the average scale growth made during a year.

Figure 2 indicates that Great Slave Lake commercial trout grow only between late May and the middle of September, with no growth at any other time. There is, in fact, a possible indication of a slight decrease in size during the winter. For "average" fish about half of the growth is made during July. Fry (1952) found much the same sort of seasonal growth in the trout of South Bay, although they differed in that the growing season was slightly longer.

The departure of the points from the curve in Figure 2 can be explained mostly as variation among individual fish as to the time when annual growth starts. The column "fish showing growth" in Table III gives some indication of the extent of this variation. Part of the variation is probably also the result of local conditions, particularly water temperatures, which tend to affect a given group of fish in the same way. For instance the point farthest from the line (below) in Figure 2 represents a sample taken where the water had been for some time appreciably colder than at any other sampling station. In fact all six points representing Station V, which is probably the slowest station to warm, were below the line in Figure 2, the only case where all the points representing any station showed a significant tendency to fall on either side of the line (nine of the ten points representing 1947 fall below the line—also a significant tendency). On the other hand in a sample of standard-gang trout (not shown) from

Fort Resolution where the water in early spring is appreciably warmer than most of the rest of the lake, the ratio AB/BC was 28 per cent on June 11, which point if plotted on Figure 2 would be farther from the line than any other point above it. These data indicate that perhaps early warming promotes early growth, whereas late warming results in late growth. In this connection note that the curve in Figure 2 is related to the water temperatures experienced by average trout, in that growth starts as soon as water temperatures are appreciably higher than in winter and that the rate increases as the temperature increases. However, growth slows down and almost stops before the temperature drops appreciably from the values associated with rapid growth earlier in the season. The variation among individual fish as opposed to variation among groups of fish can be regarded as at least partly the result of their individual temperature history.

In all suitable standard-gang trout samples the fish were grouped into three lots, those less than 5 years old, those between 5 and 10, and those more than 10 years old, and for each lot at each time and place the average AB/BC was calculated. There was no indication that age influenced seasonal growth, however the data were too scanty to make this conclusion reliable.

The considerable growth that can take place in a short time, and the variation in the time at which growth starts, made it imperative to take special precautions in interpreting samples taken in July. There was a possibility that fish which had started growing comparatively early would be mistaken for fish which had grown less than the average amount during the previous year, and had not started to grow during the year of capture, and vice versa. A very useful guide was found in the fact that only rarely does a trout appear to make less than 50 per cent as much growth in one year as it did the previous year. Hence whenever AB/BC is less than 50 per cent for any given scale, that scale can be regarded as one where the annulus for the current year has already formed. Groups of fish in which individual ratios of AB/BC range both above and below 50 per cent are almost always either distinctly bimodal or distinctly unimodal with respect to the distribution of AB/BC. Repeated comparisons of samples taken on different dates have convinced the author that, with rare exceptions, by the time the ratio AB/BC for those individuals which start growing first approaches 50 per cent, all other individuals at the same place have started growing, or at the very least show evidence of an incipient annulus. Hence, it appears that the distribution of AB/BC is unimodal at first before growth begins (no samples were taken this early), then it becomes bimodal with one mode the same as before, the other composed of low values of AB/BC and representing growing fish, finally it becomes unimodal again when all have begun growing. This knowledge has made it possible to avoid this potential source of error, and it is therefore felt that the data shown in Table III and in Figure 2 are practically unbiased in this respect. The fact that trout scales are small and that the increment, particularly in the early season, is only a small proportion of the whole scale, makes accurate measurement difficult and may have distorted the results to some extent.

In reading the scales the fish were arbitrarily assigned the date May 1 as their "birthday". Fish, considered to have formed an annulus since May 1, were recorded as age x where x was the number of annuli. Any which were interpreted as having not yet formed an annuli since May 1 were regarded as age x where $x-1$ was the number of annuli observed. In this paper "age x" is used in this sense and fish of age x are also referred to as being x years old.

GROWTH RATE

Table IV shows average size at various ages as determined from each scale sample taken. Most of the fish taken had made some growth since May 1, therefore obviously the average weight when captured must have been greater than if the fish had been exactly the designated age. To make exact comparisons

TABLE IV. The relationship between age and average weight in pounds in representative samples of Great Slave Lake commercial trout. Roman numerals indicate location (see Figure 1). Only averages based on 20 or more fish are shown.

		Age												
Sta.	Year	6	7	8	9	10	11	12	13	14	15	16	17	Fraction[a]
I	1948	...	5.0	5.5	6.3	8.6	9.6	11.0	13.8	15.1	17.7	18.7	21.6	1.00
I	1949	...	...	5.0	5.3	6.7	7.9	8.3	...	...	...	...	...	0.45
I	1952	...	5.6	6.3	6.9	7.5	8.3	...	...	...	...	...	...	0.96
II	1949	...	...	...	...	...	7.6	10.6	11.6	12.4	15.5	...	...	0.78
II	1950	...	3.8	5.3	6.2	8.1	11.1	14.2	17.8	19.3	20.3	...	...	0.70
III	1946	...	...	...	...	...	8.5	9.7	10.5	...	...	...	...	0.62
III	1949	...	...	5.1	6.1	7.5	9.7	11.5	12.7	15.9	...	...	...	0.64
III	1950	...	...	5.5	5.8	7.0	9.3	13.5	15.5	18.8	...	...	...	0.57
III	1951	...	...	4.5	5.4	6.2	9.5	...	...	...	...	...	...	0.18
III	1952	2.8	3.5	4.9	5.8	7.5	9.4	11.7	...	...	...	...	...	0.77
IV	1946	...	...	4.9	5.9	6.4	...	...	...	...	...	...	...	0.29
IV	1947	...	...	...	5.5	5.7	5.8	6.6	7.7	...	...	...	...	0.86
IV	1949	...	...	4.1	4.8	5.7	6.6	7.4	...	...	...	...	...	0.96
IV	1950	...	...	...	5.4	5.8	6.4	6.4	6.9	...	...	...	...	0.90
IV	1952	...	4.2	4.3	4.4	5.5	5.6	8.1	9.8	...	...	...	...	0.72
V	1947	...	...	...	5.4	6.3	7.5	8.0	8.6	10.6	13.3	...	...	0.79
V	1950	...	...	...	6.5	6.6	...	...	...	...	...	...	...	0.51
VI	1949	...	...	...	5.6	5.6	5.8	6.0	6.0	6.9	7.5	...	...	0.68
VI	1950	...	...	5.5	5.6	6.6	7.6	9.3	...	...	...	...	...	0.91
VI	1952	...	...	4.9	5.2	6.4	...	...	...	...	...	...	...	0.92
VII	1947	...	...	...	...	...	6.7	6.7	7.9	7.6	8.5	...	...	0.93
VII	1949	...	...	...	5.8	6.2	7.2	7.9	7.6	8.9	10.5	...	...	0.95
VII	1950	...	...	...	6.0	6.5	7.0	8.0	10.1	11.4	16.5	17.7	...	0.77
VII	1952	...	...	...	...	...	5.3	6.5	7.1	7.1	...	...	...	0.69

[a]Actual age was greater than the designated age by some fraction of a year, therefore the average weight must have been greater than at the birthday. The values listed in this row indicate the average fraction of a total year's growth made by the respective samples.

possible the estimated average proportion of the current year's growth for all the fish in each sample (mean values read off from the curve in Figure 2 and weighted according to number represented) are shown in the last line of Table IV. Suppose, for instance, that the samples at Station I for 1949 and 1952 are being compared, then it should be kept in mind that each average calculated for 1949 includes an estimated 45 per cent of the growth for the current year, whereas each average for 1952 includes about 96 per cent.

An outstanding feature of Table IV is the variability in average size at a given age. This variability was not too surprising since it had been noticed that sub-samples taken a few miles apart (within the sampling area) on the same day or on a specific spot a few days apart often differed considerably. No significance is therefore attached to individual variations.

It seems that growth rate can be best represented by grouping the data in a few categories rather than by using the data as presented in Table IV. Grouping by years fails to indicate that growth rate changed during the time under consideration, although it is interesting to note that for some unknown reason the samples tended to include particularly fast growing fish in 1950. Grouping by location indicates that samples from Stations I, II and III (in the western, non-Precambrian half of the lake) had much the same growth rate and those from Station IV, V, VI and VII (in the eastern Precambrian half of the lake) were similar to each other in growth rate but different from the other three. The data have therefore been grouped into two categories; all years at the three western stations, and all years at the four eastern stations.

These grouped data are plotted in Figure 3A. The upermost line connects the points which represent the western stations. They are plotted at ages 6.76, 7.76, 8.76 and so on because it was calculated that the fish in the sample had made an average of 76 per cent of the growth usually made in one year. The middle line connects the points which represent the eastern stations. It was calculated that fish in this sample had made 81 per cent of an average year's growth and the points were plotted accordingly. The lowest line connects points that represent average weights based on all the standard-gang fish taken in the eastern half of the lake (the fraction of seasonal growth was calculated to be 75 per cent). Similar data for standard-gang fish taken from the west half of the lake are too scanty to justify plotting. However it can be stated that, although fluctuations obscure the situation, average weights tended to be slightly higher in the west half of the lake at a given age than in the east half.

Before considering Figure 3 further the data in Tables V and VI should be examined. These tables show the range in size at each age among commercial fish, Table V for the western stations and Table VI for the eastern stations. There is a tremendous range in size at each age—for all well-represented ages some fish are five times the size of others and it is possible for the largest to be more than ten times as large as the smallest. There is, however, an obvious tendency for the upper limit, the lower limits, and the mode to become larger with age, which indicates growth at all sizes. Further examination suggests that net selection prevents the younger fish from being correctly represented, that

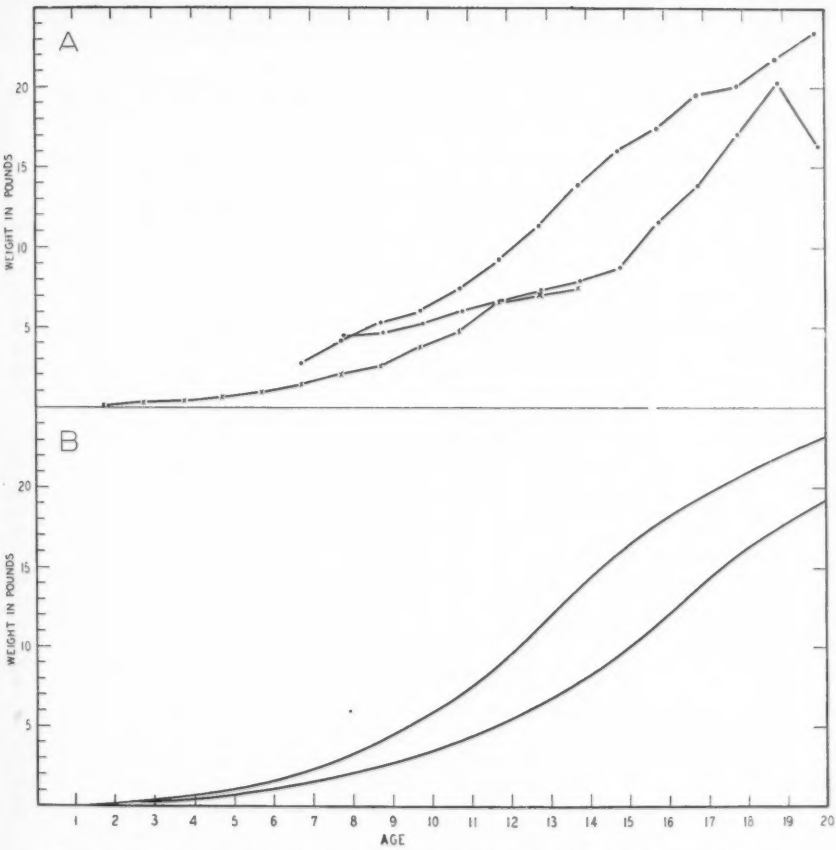

FIGURE 3. A. The relationship between age and average weight in samples of Great Slave Lake trout. Only points based on at least 15 fish are shown. *Top line*–samples taken at Stations, I, II and III. *Middle line*–samples taken at Stations IV, V, VI and VII. *Bottom line*–samples caught in standard-gangs in the east half of the lake.

B. Probable approximate age-weight relationship for average Great Slave Lake trout. *Top line*–east half of the lake. *Bottom line*–west half of the lake.

is, the nets used to take commercial fish presumably do not take trout classified as weighing 0 pounds (weight less than one-half of a pound) in sufficient quantities to have any appear in the sample, and also they apparently take less than the "expected" number of those weighing 1, 2 and perhaps 3 pounds. There seems good reason to regard all fish younger than about age 13 as subject to net selection, so that average weights of fish in the sample would be greater than the true average weights in the population.

Turning again to Figure 3, notice that a smooth curve could be drawn among the points representing commercial fish of ages 13 and over from the

TABLE V. The number of lake trout of a given age which are of a given weight in a representative sample from commercial fishermen's catches made at scale collection Stations I, II and III in the years 1946–1952, inclusive.

	Age																				
Wt.	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	25	Total
lb.																					
1	1	2	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	4
2	2	4	20	26	7	2	2	...	1	...	...	...	...	...	...	...	...	...	...	...	64
3	...	2	13	47	35	21	3	...	1	...	...	...	...	...	...	...	...	...	...	...	122
4	...	1	11	49	124	71	18	4	2	...	...	...	...	...	...	...	...	...	...	...	280
5	...	...	1	49	142	204	95	22	15	4	4	...	...	...	...	...	...	...	...	...	536
6	...	...	...	19	89	169	151	62	15	5	1	...	...	...	...	...	...	...	...	...	511
7	...	...	...	5	62	101	132	66	17	17	6	3	1	...	...	...	...	...	...	...	410
8	...	...	...	7	31	66	80	73	42	21	3	5	2	...	...	...	...	...	...	...	330
9	...	...	...	3	14	27	62	74	41	22	8	4	1	1	...	...	1	...	...	...	258
10	...	...	...	...	7	26	34	68	46	30	18	7	4	1	...	...	0	...	...	...	241
11	...	...	...	...	4	11	26	21	46	24	19	8	2	3	...	...	0	...	...	...	164
12	...	...	...	...	0	4	16	19	20	19	20	16	0	0	1	1	0	...	...	...	116
13	...	...	...	...	2	0	10	19	27	22	11	8	4	5	0	0	0	...	...	...	108
14	...	...	...	...	1	1	8	8	18	17	13	6	4	1	2	0	0	...	...	...	79
15	...	...	...	...	...	...	4	12	21	25	23	5	6	3	0	0	0	...	...	...	99
16	...	...	...	...	...	...	1	6	9	18	10	5	7	4	0	0	0	...	...	...	60
17	...	...	...	...	...	...	0	3	9	8	13	14	4	5	2	0	1	...	...	...	59
18	...	...	...	...	...	...	0	9	6	9	7	16	4	3	2	0	1	...	...	1	58
19	...	...	...	...	...	...	2	4	3	10	9	10	7	1	1	2	0	...	...	...	49
20	...	...	...	...	...	...	0	1	3	12	14	8	6	4	4	1	0	...	...	...	53
21	...	...	...	...	...	...	1	3	3	5	9	5	5	2	2	5	0	2	...	...	42
22	...	...	...	...	...	...	1	1	4	14	4	6	2	3	1	2	1	0	...	...	39
23	...	...	...	...	...	...	1	2	2	7	4	5	5	7	2	0	1	0	...	...	36
24	...	...	...	...	...	...	0	2	2	6	8	8	2	2	0	2	0	0	...	...	32
25	...	...	...	...	...	...	0	...	5	4	4	6	3	4	0	2	0	0	...	...	28
26	...	...	...	...	...	...	1	...	1	1	5	5	5	2	4	0	0	0	...	...	24
27	...	...	...	...	...	...	...	...	1	2	3	3	3	2	0	2	1	0	1	...	18
28	...	...	...	...	...	...	...	...	1	1	2	1	1	3	0	1	0	1	...	...	11
29	...	...	...	...	...	...	...	...	0	2	2	0	2	0	0	0	0	0	...	...	6
30	...	...	...	...	...	...	...	...	1	0	3	2	3	1	1	0	0	0	...	...	11
31	...	...	...	...	...	...	...	...	...	2	0	3	1	0	1	0	0	1	...	...	8
32	...	...	...	...	...	...	...	...	...	1	2	1	0	1	2	0	1	0	...	...	8
33	...	...	...	...	...	...	...	...	...	...	1	0	0	0	...	0	0	0	...	...	1
34	...	...	...	...	...	...	...	...	...	...	0	0	1	0	...	0	1	0	...	...	2
35	...	...	...	...	...	...	...	...	...	...	0	1	1	0	...	1	...	0	...	...	3
36	...	...	...	...	...	...	...	...	...	...	0	...	0	0	...	1	...	0	...	...	1
37	...	...	...	...	...	...	...	...	...	...	2	...	1	1	...	...	...	0	...	...	4
55	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	1
Total	3	9	45	206	518	703	648	479	362	308	228	161	87	59	25	20	8	5	1	1	3,876

TABLE VI. The number of lake trout of a given age which are of a given weight in a representative sample from the Great Slave Lake commercial fishermen's catches made at scale collection Stations IV, V, VI and VII in the years 1946–1952.

	Age																		
Wt.	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	25	Total
lb.																			
2	1	1	7	5	4	1	...	...	...	...	...	...	...	...	...	...	...	...	19
3	1	15	45	24	13	11	2	...	...	...	...	...	...	...	...	...	...	...	111
4	1	26	133	172	92	53	26	11	8	...	...	1	...	...	...	...	...	...	523
5	0	27	133	250	233	181	136	59	23	9	2	0	...	...	...	...	...	...	1,053
6	1	8	66	188	217	202	164	106	63	19	2	0	1	1	...	...	...	...	1,038
7	...	5	23	67	150	145	132	102	55	22	5	5	0	0	...	...	...	...	711
8	...	1	4	28	60	84	70	62	36	23	12	3	0	1	1	...	...	...	385
9	...	...	2	6	33	47	76	54	25	14	5	3	0	0	0	...	...	...	265
10	...	...	...	2	14	32	34	27	20	17	7	4	0	2	1	...	...	...	160
11	...	...	...	2	13	23	19	17	14	11	12	1	2	0	1	1	...	...	116
12	...	...	...	1	3	16	15	8	7	7	7	4	0	1	0	1	...	...	70
13	...	...	...	...	1	5	6	10	11	8	5	3	1	1	2	0	...	...	53
14	...	...	...	...	1	4	6	8	8	9	2	2	3	1	0	0	...	...	44
15	...	...	...	...	0	0	8	7	6	8	4	2	0	4	0	0	2	...	41
16	...	...	...	...	1	2	5	2	5	8	6	4	1	0	1	0	0	...	35
17	...	...	...	...	...	...	3	7	2	8	8	3	1	1	1	0	0	...	34
18	...	...	...	...	...	...	0	2	4	0	3	5	2	1	1	0	0	...	18
19	...	...	...	...	...	...	1	2	3	6	4	1	1	2	0	0	0	1	21
20	...	...	...	...	...	...	2	1	4	3	0	3	2	0	0	0	0	...	15
21	...	...	...	...	...	...	1	1	1	3	4	2	1	1	0	0	0	...	14
22	...	...	...	...	...	...	0	1	2	2	3	1	2	1	0	1	0	...	13
23	...	...	...	...	...	...	2	0	0	1	4	0	0	0	0	...	0	...	7
24	...	...	...	...	...	...	1	1	0	2	3	2	1	1	0	...	0	...	11
25	...	...	...	...	...	...	...	0	0	1	0	1	0	0	0	...	1	...	3
26	...	...	...	...	...	...	...	0	0	0	0	1	1	1	0	...	0	...	3
27	...	...	...	...	...	...	...	1	0	81	82	81	0	0	1	...	0	...	6
28	...	...	...	...	...	...	...	...	0	2	1	1	1	1	1	...	0	...	7
29	...	...	...	...	...	...	...	...	0	1	0	0	1	...	...	...	0	...	2
30	...	...	...	...	...	...	...	...	0	0	1	0	0	...	...	...	0	...	1
31	...	...	...	...	...	...	...	...	1	1	...	1	1	...	...	...	0	...	4
32	...	...	...	...	...	...	...	...	...	1	...	3	0	...	...	...	0	...	4
33	...	...	...	...	...	...	...	...	...	...	...	3	0	...	...	...	1	...	4
34	...	...	...	...	...	...	...	...	...	...	...	1	0	...	...	...	0	...	1
37	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	0	...	1
38	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	0	...	1
45	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	1
Total	4	83	413	745	835	806	709	489	298	187	102	61	24	20	10	3	5	1	4,795

eastern stations. The fact that the points tend to deviate from such a line, particularly at higher values (i.e., those represented by fewer fish), is not surprising in view of the tremendous size range involved in each average. The points which represent age–8 and younger standard-gang fish from the eastern stations also form a smooth curve which, if extrapolated, is continuous with the above-mentioned cure. Although the possibility of net selection among standard-gang fish cannot be eliminated, the position of these points suggests that it is probably a minor factor. Growth in the east half of the lake can therefore be represented by a smooth curve something like the lower curve in Figure 3B. The fact that observed average weights fall consistently above this line over the middle part of its range is regarded as an effect of net selection. Similarly the upper line in Figure 3B, can be regarded as an approximation to the growth curve in the west end of the lake, since at its upper end it would fit those points where net selection is presumed not to influence average size caught, while its lower end fulfils the condition that values be slightly higher than on the other curve. .

Evidently fish in the west half of the lake at first grow considerably faster than those in the east half, and are about 75 per cent larger at any age between ages 9 and 15. Trout in the west end may experience higher average water temperatures which would probably increase rate of growth. There appear to be less trout per unit area in the west half, which would also probably encourage growth.

Great Slave Lake trout grow considerably faster than do those of Great Bear Lake (Miller and Kennedy, 1948). They grow at about the same rate as trout farther south although slightly slower than the most southerly, fastest growing ones (Martin, 1952). The growth rates indicated here differ considerably from those given by Rawson (1947) for Great Slave Lake, probably because his rates were based on only a few specimens.

MORTALITY RATE

Mortality rates in fish populations can be estimated if the ages of random samples are known. The technique has been reviewed by Ricker (1948). The principle involved is as follows: in any representative sample if those fish which are not large enough to be fully vulnerable to the fishing gear are disregarded, the number of fish of each age tends to be less than the number one year younger. The usual explanation is that the number of fish in any given year-class diminishes from year to year as a result of deaths from various causes (note that fluctuations in year-class strength tend to obscure this effect). The observed rate of decrease within a large-enough sample is regarded as representing annual mortality rate in the population, that is, the proportion of fish which die annually. In practice, mortality rates are determined graphically from "catch curves". Catch curves result from plotting the logarithms of numbers of fish of a given age against age.

Table VII gives all the data available for determining mortality rates for Great Slave Lake commercial trout, that is, the number of fish of each age taken

TABLE VII. The number of fish of each age in representative samples of Great Slave Lake commercial trout.

		Age																	
Sta.	Year	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Over 20
I	1948	1	0	3	31	78	119	89	87	77	69	45	33	22	20	9	8	2	1
I	1949	0	0	0	7	29	37	39	40	31	17	17	15	7	7	1	1	2	2
I	1952	0	0	2	28	132	144	94	31	9	3	3	0	1	0	0	0	0	0
II	1949	0	0	0	2	8	11	16	24	26	30	21	22	12	7	4	2	2	3
II	1950	1	2	7	25	38	68	62	56	53	65	61	36	17	6	4	1	1	0
III	1946	0	0	0	0	3	16	19	22	26	21	15	15	11	9	1	7	1	0
III	1947	0	0	1	6	11	15	10	7	4	5	1	4	1	0	0	0	0	1
III	1949	0	2	4	19	49	69	85	85	72	45	29	16	9	5	3	0	0	0
III	1950	0	0	1	14	40	85	101	62	30	33	21	14	4	4	3	1	0	0
III	1951	0	1	1	4	28	29	36	23	6	10	10	4	1	1	0	0	0	0
III	1952	1	4	26	70	102	110	97	42	28	10	5	2	2	0	0	0	0	0
IV	1946	0	0	2	6	27	38	22	16	11	5	3	1	3	1	1	0	0	0
IV	1947	0	0	0	0	6	26	59	51	55	35	11	11	10	6	1	1	1	2
IV	1949	0	0	0	11	105	153	90	57	26	17	7	10	4	2	1	1	0	1
IV	1950	0	0	0	3	13	35	70	60	42	21	12	6	1	1	0	0	0	0
IV	1952	0	0	0	21	85	116	80	53	45	24	15	2	3	1	1	2	0	0
V	1947	0	0	0	4	13	23	50	77	78	41	27	24	10	9	1	2	0	2
V	1950	0	0	0	8	19	31	28	19	12	2	2	1	0	0	0	0	0	0
VI	1949	0	0	0	1	12	35	57	111	111	99	71	30	9	13	3	2	5	3
VI	1950	0	0	1	10	72	139	160	84	37	18	7	6	1	1	3	0	0	0
VI	1952	0	0	1	13	33	42	28	12	2	0	1	1	0	0	0	0	0	0
VII	1947	0	0	0	0	0	2	19	43	68	73	33	25	14	5	2	5	1	0
VII	1949	0	0	0	5	9	46	68	81	89	68	46	30	12	10	5	5	3	0
VII	1950	0	0	0	1	18	53	87	98	94	51	33	28	25	8	6	0	0	1
VII	1952	0	0	0	0	1	6	17	44	39	35	30	12	10	4	0	2	0	0

in representative samples at various times and places. Figure 4 shows a series of catch curves based on these data. Notice that only points representing at least five fish are used in these catch curves, which keeps the graphs to a reasonable size without omitting any essential details. There are blank squares in Figure 4 because: (1) sampling was deliberately curtailed in 1948 and in 1951, (2) very little fishing was done at Station V except during the years when samples were taken, (3) fishing at Station I in 1950 lasted for too short a time to permit sampling, (4) the remaining blanks represent no fishing during the year at the station.

RELATIVE STRENGTH OF YEAR–CLASSES

Suppose there is a population of fish in which the 1930 year-class is particularly strong, and suppose this population is sampled for several years starting

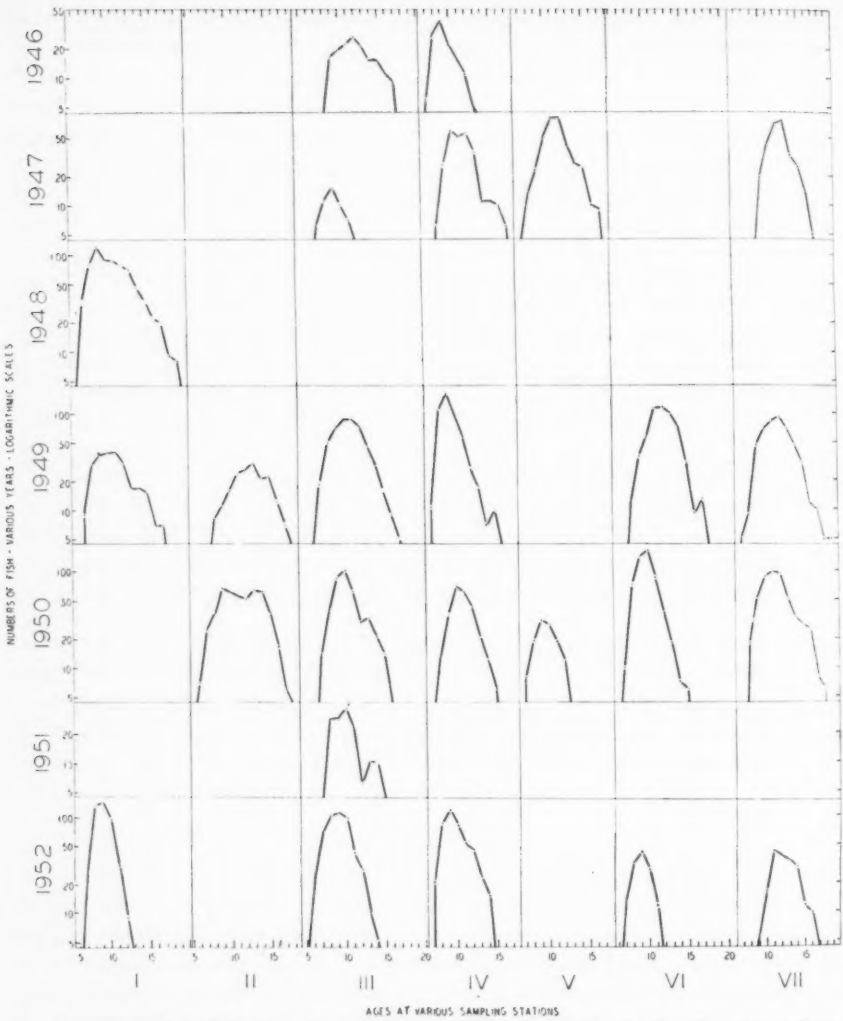

FIGURE 4. The catch curve for each sample of commercial trout taken from Great Slave Lake. Each row represents the samples taken in a given year, each column the samples taken at a given station (see Figure 1). Only points representing five or more fish are used.

in 1946, and suppose also that the fish are fully vulnerable to the gear by the time they reach age 15. If catch curves are now plotted for the various years and the trends of the points on the right limbs noted, then because the 1930 year-class is particularly strong the point representing age–16 fish will be particularly high in the 1946 sample, that representing the age–17 fish particularly high in the 1947 sample, that representing the age–18 fish particularly high in

the 1948 sample and so on. Similarly a particularly weak year-class would be represented by a series of points which fall consistently below the general trend. There is no indication in Figure 4 that at any location the points representing any year-class tend to fall consistently either above or below the general trend in this fashion. Neither would combining samples from different localities show such a trend. It is therefore concluded that all year-classes of Great Slave Lake trout are of approximately equal strength.

Possible Effects of Exploitation

Ricker (1948) shows that if there has been a recent increase in mortality rate then the right limb of a catch curve must be concave, that is, the slope of the right limb must be steeper just to the right of the dome than it is further to the right. He also shows that the concavity moves to the right with time. Examination of the curves in Figure 4 fails to show any consistent indication of such concavity. Ricker (personal communication) has pointed out that since, in Figure 4, most of the catch curves have only three to five years represented to the right of the dome, concavity resulting from the extra mortality caused by fishing would not necessarily be easy to distinguish; and further, that the most noticeable effects in this case should be (1) a steepening of the slopes between corresponding ages and (2) a tendency for the mode to shift to a younger age. Figure 4 gives the impression that both tendencies are acting. However, special attention should be given to the samples from Station IV because until 1949 its surrounding fishing grounds were by far the most heavily exploited of all. If the apparent tendencies in Figure 4 are to be attributed to exploitation, then the greatest increase in slope and the greatest shift in mode should appear at Station IV where early exploitation was greatest. Actually these tendencies are least at Station IV. This fact casts suspicion on any conclusion that the apparent changes are the result of exploitation. Since subsamples taken at a given station within a few days of one another sometimes differ considerably in each of these respects, the apparent trends in Figure 4 could also be attributed to the vagaries of sampling, including the possibility that changes in fishing gear or in technique are somehow responsible. It was noted in the preceding section that the 1950 samples tended to include particularly fast growing fish—no doubt also the result of the vagaries of sampling. It is perhaps pertinent to record that at Station I all of the 1948 sample and about half of the 1949 sample were taken during the winter when fishing techniques differ considerably from those used in the summer when all other samples were taken.

To overcome the difficulties which arise because each curve in Figure 4 is based on considerably fewer fish than is desirable, the data in Table VII were combined in various ways and the resulting catch curves (not shown) plotted. Note that combining several samples always results in at least ten years being represented in the right limb. None of the resulting curves show concavity in the right limb, in fact they tend to show convexity which is generally regarded as indicating an unexploited population. It is true that the slopes tend to steepen and that the modes tend to shift to younger ages when data are combined by

years, which could be regarded as indicating an effect of exploitation although the effect cannot be regarded as great since the slopes of the right limbs indicate the following comparative value for mortality rate among the fully vulnerable fish: 1946–45 per cent; 1947–45 per cent; 1948–41 per cent; 1949–41 per cent; 1950–49 per cent; 1951–48 per cent; and 1952–53 per cent. Nevertheless the fact that the curves representing the latest years have convex right limbs is evidence that exploitation has had little effect. It therefore seems justifiable and desirable to combine the data from several stations for all years. Such a combined sample can be regarded as representing the general area for the whole time, particularly since the number sampled at each station was roughly proportional to the apparent abundance in that part of the lake. The combined sample can also be regarded as approximately representing conditions before fishing began, although perhaps *slightly* modified as a result of exploitation.

Differences between Parts of the Lake

Figures 5A and 5B show the catch curve for the combined data from Stations I, II and III and from Stations IV, V, VI and VII, respectively. All points in Figure 5 are at ages 4.25, 5.25, 6.25, etc., because the fish were caught, on the average, about three months after May 1. In the two catch curves just mentioned, notice that the domes differ in shape. An explanation for this phenomenon arises from Rawson's (1951) hypothesis that ". . . much of the lake trout reproduction occurs in the east arm and that there is a general migration to the west during the life of the fish". Such a migration, if not completed by some of the fish until they are relatively old, could produce a difference in shapes of domes such as is exhibited by the two catch curves, because some of the fish which eventually contribute to the right limb of A are still contributing to the dome of B, hence making the dome of B too high and the dome of A too low with respect

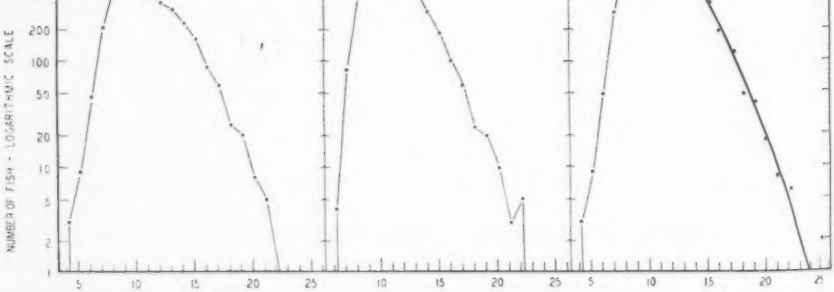

Figure 5. Catch curves for all Great Slave Lake trout in the samples from 1945 to 1952, inclusive: (A) taken at Stations I, II and III (western part of the lake); (B) taken at Stations IV, V, VI and VII (eastern part of the lake); (C) taken at all stations combined.

to certain ages (say ages 10 to 15). These year-classes are even more deficient in A than the difference in shape indicates, since A represents western fish which are faster growing, hence presumably vulnerable to the fishing gear at an earlier age. Earlier vulnerability apparently accounts for the larger numbers of age–8 and age–9 fish in A as compared with B. The shape of the dome in A cannot be regarded as evidence of a change in mortality rate because the area represented by these data was not exploited nearly as heavily as that represented by B, and B failed to have a similar shape. The difference between the two curves is therefore regarded as further evidence for Rawson's hypothesis.

Representative Catch Curve

It is evident that mortality cannot be properly assessed in either half of the lake, by itself, because of the effect of migration on the shape of the catch curve. Therefore all the data were combined to give the catch curve shown in Figure 5C. The points on the right limb tend to form a slightly convex curve. A smooth curve was fitted to these points by drawing the arc of a large circle through them. There is no particular reason for choosing the arc of a circle other than that it fits well and has the advantage that it can be extrapolated without introducing personal bias.

Change in Catchability with Age

It is interesting to see whether vulnerability to the gear increases in a symmetrical manner as Ricker (1948) postulates it may. The extrapolated smooth curve of Figure 5C indicates 2,210 age–11 fish, compared with 1,285 actually captured, indicating that fish of this size are only 58 per cent as vulnerable to the gear as they will eventually become. It also indicates 3,360 age–10 fish compared with 1,483 actually captured indicating 44 per cent vulnerability. By similar procedures the following pairs of values were calculated; 75 per cent at age 12 versus 30 per cent at age 9; 88 per cent at age 13 versus 13 per cent at age 8; 94 per cent at age 14 versus 3 per cent at age 7; and 102 per cent at age 15 versus 0.3 per cent at age 6. Each pair very nearly totals 100 per cent–the deviations are easily explained by the vagaries of sampling–and it is apparent that vulnerability to the gear does increase in a symmetrical way. Smooth curves which depart from the specific arc selected for Figure 5C by even a barely perceptible amount tend to indicate a considerably less symmetrical increase in vulnerability. The precise curve used was chosen partly because it implied maximum symmetry in this respect.

The curve indicates that Great Slave Lake trout are not fully vulnerable to the gear until age 15. However, they are probably nearly enough fully vulnerable at ages 13 and 14, that the growth curves in Figure 3B can be regarded as essentially unaffected by the assumption that net selection does not influence average weight at these ages. The departure of the left limb and dome of Figure 5C from the extrapolated curve is, of course, an actual demonstration of the net selection postulated in connection with Tables V and VI. It is interesting to note that the three age–4 fish captured represent only 0.01 per cent of the

age–4 fish indicated by the curve, in other words only about one age–4 fish is captured for every 10,000 that would be captured if nets caught small fish as efficiently as they catch big ones.

The convexity of the right limb of Figure 5C might be attributed to a decreasing vulnerability to the gear as size increases. In this regard it is useful to study Rawson's (1951) Figure 7 which shows the size of Great Slave Lake trout caught in various sizes of mesh. This figure shows that the 1½-inch mesh catches some fish which are almost as big as the biggest caught in 5½-inch mesh (no significance can be attached to the fact that none were actually as big). In fact, a consideration of the relative numbers of each size available for capture indicates that the various small-meshed nets were more efficient in taking fish of size that could only have been caught by their mouth parts than they were in taking those sizes usually caught by passing part way through the mesh. Figure 5C indicates that fish must be at least age 15 to be fully vulnerable to the gear, and Tables V and VI indicate that all age–15 fish weigh at least 5 pounds. Since trout over 4 pounds are too large to be caught by passing partway through the mesh, the inevitable conclusion is that gill-nets are most efficient in taking trout when the trout are too big to pass partway through and can only be caught by their mouth parts. It seems unlikely that big fish are caught by their mouth parts less efficiently than are medium-sized fish, hence the convexity probably cannot be attributed to vulnerability to the gear decreasing with age.

Change in Mortality Rate with Age

The fact that the curve is convex can be regarded as indicating that mortality rate increases with age. By drawing tangents to the curve, finding their slopes, and using a technique outlined by Ricker (1948), the annual mortality rates at various ages can be calculated. For instance, when fish are exactly 15 years old the mortality rate is 39 per cent, which means that of all the fish which become 14½ years old, 39 per cent dies during the year and only 61 per cent become 15½ years old. Other calculated mortality rates are shown in Table VIII. Since there has probably been little change in mortality rate since

Table VIII. Annual mortality rates calculated from the curve of Figure 5C including the extrapolated curve.

Age	Annual mortality	Age	Annual mortality	Age	Annual mortality	Age	Annual mortality
	%		%		%		%
0	...	7	31[a]	14	38	21	52
1	27[a]	8	32[a]	15	39	22	56
2	28[a]	9	32[a]	16	40	23	60
3	28[a]	10	33[a]	17	42	24	65
4	29[a]	11	34[a]	18	44	25	72[a]
5	29[a]	12	36[a]	19	46	26	80[a]
6	30[a]	13	37	20	49	27	100[a]

[a]Since these values are derived by extrapolation they must be used with caution and the caution should increase with greater extrapolation. At the youngest ages (say less than age 6) it is unlikely that they will even approximate the truth.

commercial fishing began in 1945, *these values are good approximations to the natural mortality rates which prevail in one unexploited population of trout.*

It is interesting to note that convex curves also would fit the points on the right limbs of Figures 5A and 5B, and that the mortality rates which could be calculated from these curves are approximately the same at any given age of commercial-sized fish as those calculated from 5C. A curve through 5B would indicate mortality rates about 1 per cent higher and a curve through 5A would indicate mortality rates about 1 per cent lower than 5C indicates.

THEORETICAL DISCUSSION

The extrapolated curve of Figure 5C leads to some very interesting and useful speculation, particularly since it deals with a population which is almost unexploited. For convenience consider a unit of the population represented by the number of fish involved in Figure 5C, that is, a unit where the number in each age-group is such that the observed mortality rates will, on the average, reduce that age-group to one fish at exactly age 23.9.

Table IX shows the data and the calculations required. All trout are

TABLE IX. Theoretical calculations about a unit of the Great Slave Lake trout population.

0	1	2	3	4	5	6	7	8
Age	Percentage mature	Percentage producing eggs	Av. wt.	Av. egg count	Av. no. eggs per fish	No. of fish	No. of eggs	Biomass
			lb.					*lb.*
0	0	0	0.05	...	...	104,000	0	5,200
1	0	0	0.1	...	...	76,000	0	7,600
2	0	0	0.3	...	...	55,000	0	16,500
3	0	0	0.5	...	...	39,000	0	19,500
4	0	0	0.8	...	...	28,600	0	22,880
5	3	0.75	1.2	900	6.8	20,100	136,680	24,120
6	14	3.5	1.7	1,400	49	14,200	695,800	24,140
7	26	6.5	2.3	1,900	124	9,800	1,215,200	22,540
8	42	10.5	3.1	2,600	273	6,700	1,829,100	20,770
9	65	16.25	4.2	3,500	569	4,600	2,617,400	19,320
10	97	24.25	5.3	4,400	1,067	3,030	3,233,010	16,059
11	100	25.0	6.7	5,600	1,400	1,990	2,786,000	13,333
12	100	25.0	8.4	7,000	1,750	1,280	2,240,000	10,752
13	100	25.0	10.3	8,400	2,100	810	1,701,000	8,343
14	100	25.0	12.2	9,700	2,425	490	1,188,250	5,978
15	100	25.0	14.0	10,900	2,725	300	817,500	4,200
16	100	25.0	16.0	12,200	3,050	179	545,950	2,864
17	100	25.0	17.8	13,300	3,325	102	339,150	1,816
18	100	25.0	19.3	14,100	3,525	57	200,925	1,100
19	100	25.0	20.6	14,700	3,675	31	113,925	639
20	100	25.0	21.6	15,300	3,825	16	61,200	346
21	100	25.0	22.6	15,900	3,975	6.8	27,030	154
22	100	25.0	23.6	16,400	4,100	3.3	13,530	78
23	100	25.0	24.5	16,900	4,225	1.4	5,915	34
					Totals	366,296	19,767,565	248,266

assumed to spawn at the same time, the time is assumed to be one-half year after the common birthday, and the calculations are made as of that instant. Age–0 fish are therefore one-half of a year old, age–1 fish are 1½ years and so on (called hereafter age one-half, age 1½, and so on). Column 1 of Table IX shows the proportion of fish in the population which are mature. The values given were read off from the curve (not shown) used to get the values given in the first column of Table II. Column 2 is the proportion of the population which produces eggs in any given year. It is derived from column 1 by dividing each value by 4, on the basis of data given in an earlier section which show that approximately one-half of the population is females, and that of those about one-half spawn in any given year. Column 3 shows average weights at various ages (at ages ½, 1½, 2½, etc.) as derived from an average of the two growth curves of Figure 3B. Column 4 shows the average number of eggs per spawning female. It is calculated on the assumption that the general relationship of egg count to body weight is a species characteristic affected to only a minor extent by local conditions. The general relationship between trout weight and fecundity was derived from data published by Fry (1949) and Carlander (1950). The egg counts shown in column 4 are values which this general relationship indicates correspond to the respective average weights of column 3. Column 5 is derived by multiplying the values in column 2 by those in column 4 and represent the number of eggs available per fish at each age. Column 6 represents values read off from the extrapolated curve of Figure 5C. Column 7 represents the calculated number of eggs available for spawning from said fish and is derived by multiplying the values given in column 5 by those given in column 6. Column 8 represents biomass, that is, the total weight of all the fish in each year-class, and is derived by multiplying the values in column 3 by those in column 6.

The total of column 7 indicates that about 20 million eggs are available for spawning. As the first line of column 6 indicates, they result in about 104,000 fish one year later. This represents a "mortality" of about 99.5 per cent for that year, which does not seem unreasonably high considering that it includes those eggs available for spawning but not actually spawned, and eggs spawned but not fertilized, as well as egg mortality and fry mortality. Alternatively, extrapolation of the curve of Figure 5C could be regarded as not correctly representing mortality rate among the youngest fish, and instead that mortalities were actually higher for them. For instance, if average mortality rate between age 1½ and age 2½ were 40 per cent instead of 28 per cent, and if between ages ½ and 1½ it were 80 per cent instead of 27 per cent, then "mortality" from available eggs to age ½ would be 97.5 instead of 99.5. In view of the present ignorance regarding early mortality of wild trout either assumption is equally acceptable. However, it is evident that major departures from the values given in Table VIII would lead to inconsistencies or be contrary to either or both of the following principles which seem to apply to mortality rates among animals in general: (1) that mortality rates generally do not change abruptly or erratically; and (2) that mortality rate is generally considerably higher during the very earliest stages than during most of the life span. It is therefore apparent that all the data presented in this paper on Great Slave Lake trout are consistent.

The sums of columns 6 and 8 lead to the following statement. For every Great Slave Lake trout which survives for 24 years, there are (exclusive of fertile eggs and newly hatched fish) roughly 300,000 to 400,000 trout weighing a total of roughly 200,000 to 300,000 pounds in the lake at any given time.

From column 7 it is apparent that about one-half of the spawning is done by fish that are less than 11 years old, hence more than 50 per cent of the spawning is done by fish too small for the gear to catch them efficiently. It therefore seems extremely unlikely that the present fishery could materially decrease the strength of future year-classes by its removal of potential spawners.

Column 8 shows that a given year-class has its maximum weight at about age 6, although the gain by growth is more or less balanced by loss from deaths over the whole range of ages 3 to 9. Year-classes are reduced to less than 20 per cent of their maximum possible weight of fish flesh before they are fully vulnerable to the gear. This could be regarded as an indication that a considerably smaller mesh size should be fished in order to have gear to which trout are fully vulnerable at that age when a year-class can make its maximum contribution in weight of fish. However, further study shows that a year-class has its maximum weight when its is composed of a large number of small fish—too small to be marketed in most cases. It is therefore obvious that the question of whether mesh size should be reduced and, if so, what new size should be established is not a simple one.

SUMMARY

1. Observations were made on a newly exploited population of lake trout, mostly fish taken in the commercial catch. Ages were determined on 9,215 fish.

2. The length–weight relationship is described.

3. Fish of both sexes mature at any time between ages 5 and 11 when they are between 15 and 23 inches long and weigh between 1.4 and 5 pounds.

4. The sex ratio is approximately 1:1.

5. Only about one-half of the mature females spawn each year.

6. There is practically no growth except between the first of June and the middle of September, and about half of the year's growth is made during July.

7. There is a tremendous size range at any given age and net selection results in the capture of only the largest individuals among the younger fish.

8. Growth rate is considerably faster in the west half of the lake than in the east half.

9. Average growth rate in Great Slave Lake is considerably faster than in Great Bear Lake and about the same as or slightly slower than in more southerly lakes.

10. All year-classes are probably of approximately equal strength.

11. Mortality rate did not increase by much as a result of seven years of commercial fishing. This is the basis for regarding the population as relatively unexploited.

12. There is further evidence to support Rawson's theory that most of the successful trout spawning is done in the east end of the lake, and that a large proportion of the trout found in the west end have migrated there.

13. The catch curve for all samples combined is convex in its right limb which indicates that mortality increases with age among fully exploited fish.

14. Annual mortality rate is about 33 per cent at age 10, 39 per cent at age 15, and 49 per cent at age 20. *These values can be regarded as approximations to mortality rates in an unexploited population.*

15. Some probable characteristics of the population at early ages are considered.

16. Biomass is probably greatest at about age 6, although it is probably more or less at its maximum from ages 3 to 9.

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The Anomaly of Mean Sea Level in Seymour Narrows, B.C.[1]

By G. Wilfred LaCroix[2] and John P. Tully[3]

ABSTRACT

During surveys of the tides and tidal currents in Seymour Narrows (1945 to 1950) the Canadian Hydrographic Service noted that there was a depression of mean sea level of the order of half a foot. There is a considerable fall of sea level along the Narrows and the square of the velocity of the current is proportional to this hydraulic head. The anomaly is a necessary consequence of the velocity, and it can be predicted from either the tidal or the tidal-current data. The annual net transport of water through the Narrows is seaward and is about five times as great as the discharge of the Fraser River.

CONTENTS

Introduction	853
The tides and tidal currents	855
Observed sea levels in Seymour Narrows	861
The anomaly of mean sea level	863
Calculation of the anomaly from tidal height data	863
The tidal currents	866
Calculation of the anomaly from tidal current data	875
Transport and discharge	881
Conclusions	881

INTRODUCTION

The northern approaches to the Strait of Georgia consist of three channels which are connected by a number of cross channels forming a maze of islands and waterways. The narrowest part of the main channel, which is adjacent to Vancouver Island, is called Seymour Narrows (Fig. 1). Extending from Port Hardy on the ocean approach in the north to Cape Mudge at the Strait of Georgia entrance in the south (Fig. 2), the main channel is the seaway used by most coastwise shipping and numerous ocean-going vessels. It may be designated as Johnstone Strait, although various names are applied to particular reaches.

Seymour Narrows contains the world's fastest tidal currents which attain velocities of 10 to 15 knots at strength and are violently turbulent (Fig. 1). Although nearly half a mile wide, navigation of the Narrows is treacherous owing to the ever-changing currents, the violent turbulences and to Ripple Rock, a pinnacle in mid-channel which ships must pass. When the tidal stream is running at strength only powerful ships may safely attempt the passage, all others await the quotidinial ten-minute periods of slack water or else go through within an hour before or after slack water when the current velocity is generally less than 5 knots. This passage is the principal navigational danger in the otherwise serene inland route along the coast of British Columbia.

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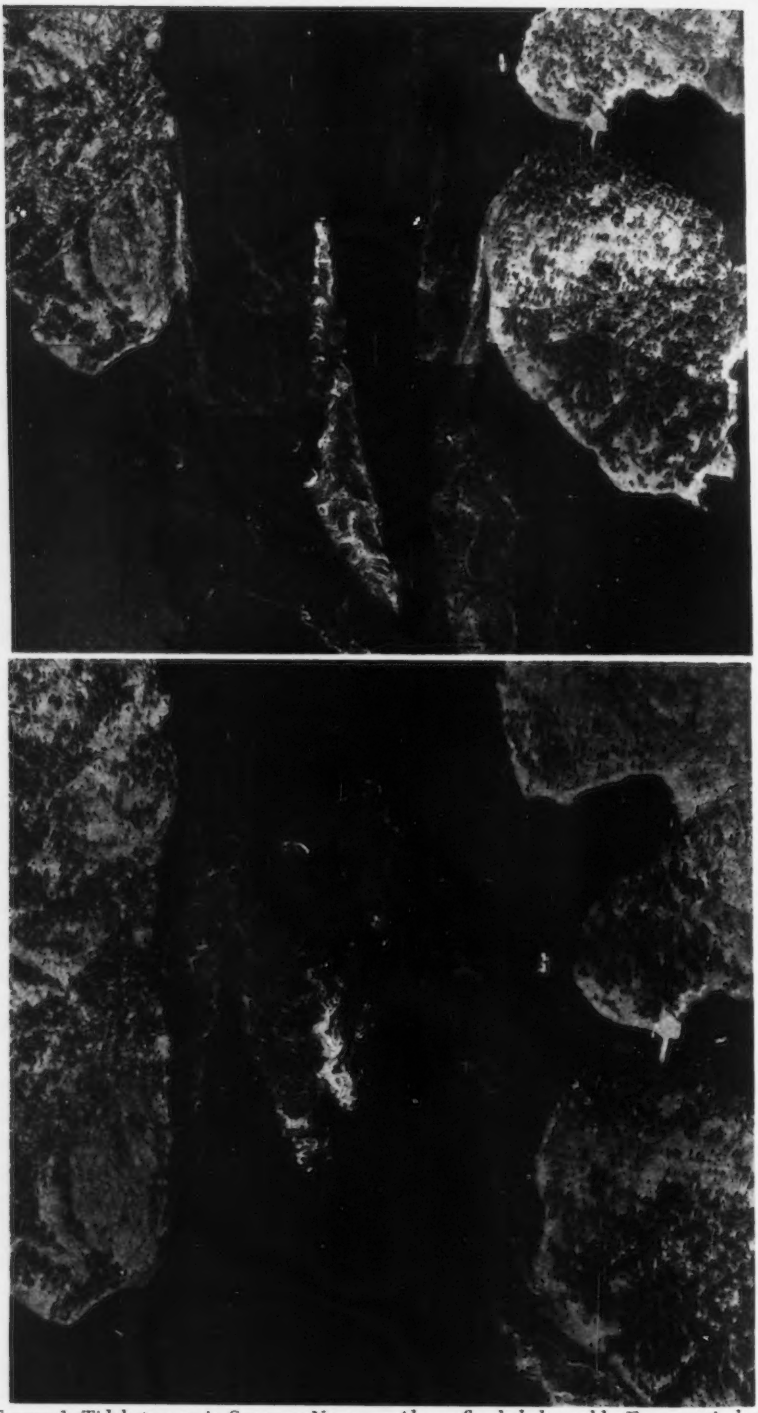

FIGURE 1. Tidal streams in Seymour Narrows. *Above*, flood; *below*, ebb. From vertical air photographs, by courtesy of the Royal Canadian Air Force.

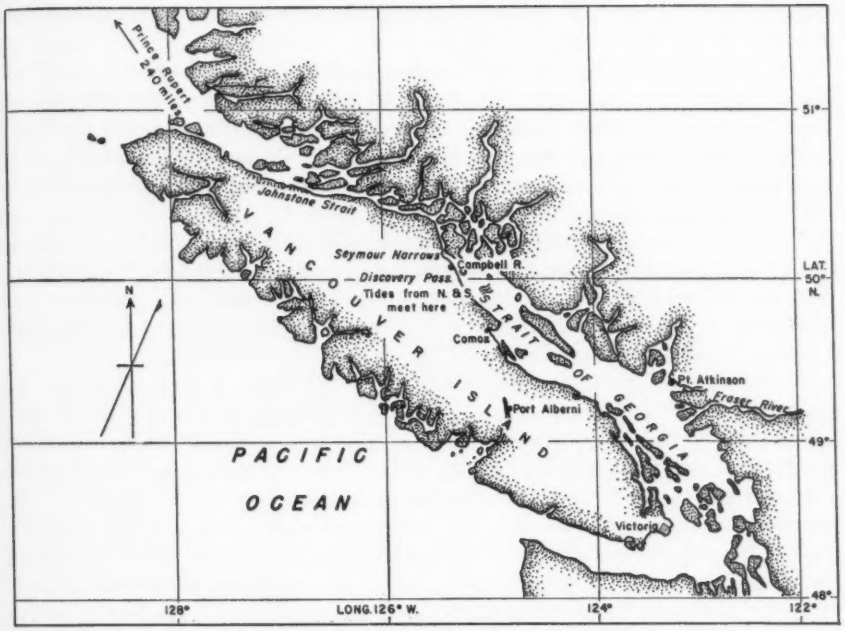

FIGURE 2. Chart of Vancouver Island and adjacent shores.

The first recorded passage through the Narrows [1] was made by Captain Vancouver with his vessels, H.M.S. *Discovery* and *Chatham*, when he circumnavigated Vancouver Island in 1792. From then until 1846 the place name shown on the charts was Yuculta (Eucluetaw) Rapids, after the tribe of Indians residing in the vicinity of Cape Mudge. The present name honours Rear Admiral Sir George Francis Seymour, G.C.H., who was in command of the Pacific Coast station (Esquimalt) from 1844 to 1848.

As is frequently the case with well known and respected dangers, there have been very few disasters. On June 15, 1875 the U.S.S. *Sarnac* was totally lost when it struck Ripple Rock and several other ships have been seriously damaged in the years since. Occasionally small boats have been lost in the whirlpools. However, except for infrequent accidents such as these, vessels both large and small have successfully navigated the passage for more than a century.

In 1944 and 1945 attempts were made to blast Ripple Rock out of the channel but these were unsuccessful.

THE TIDES AND TIDAL CURRENTS

The general aspect of the tides in Johnstone Strait and the currents in Seymour Narrows may be obtained from an examination of the Tide Tables [2]. Computations based on these have limited accuracy, since the tides at various positions must be deduced from the average differences at far-distant reference

points. However, such an examination provides the necessary background for the study of the data in Seymour Narrows.

The Tide Tables list the time and height of the high and low tide levels at Prince Rupert, to which the tides north of Seymour Narrows are referred; at Sand Heads (later Point Atkinson) in the Strait of Georgia, to which the tides south of the Narrows are referred; and at Seymour Narrows. They also list the time and velocity of the maximum flow (flood and ebb) in the Narrows, and the time of slack water.

Along the ocean coast of Vancouver Island the semi-diurnal tidal rise is very nearly synchronous (within 15 minutes) and from this impulse, tidal waves progress around both ends of the Island (Fig. 2). The sea level differences are compensated in Seymour Narrows, but the opposing flows meet in the Strait of Georgia somewhat north of Comox.

The southern part of the primary wave undergoes a marked change in character as the impulse progresses through the Strait of Georgia. In partial explanation of this it may be said that the estimated period of oscillation of the Strait of Georgia (245 minutes) is very nearly one-third the average tidal period (745 minutes); consequently a standing wave develops in this basin which alternately damps and reinforces the progressive wave. This causes a marked diurnal inequality especially in the low water levels, a marked alteration in the phase incidence and a greater range of tide than is observed on the ocean coast or in the northern or southern approaches to the Strait of Georgia. In the northern part of this area where the resultant wave is relatively unrestricted, high water is nearly synchronous and there is very little current. The channel from Cape Mudge to Seymour Narrows is short and so this wave is impressed on the Narrows without much alteration.

The northern part of the primary tidal impulse traverses the length of Johnstone Strait (about 100 nautical miles) before arriving at Seymour Narrows. The character of this tide is shown in Figure 3. At the ocean, represented by Port Hardy, it is semi-diurnal and moderately declinational in type. Progressing southward at a rate of some 60 knots, the amplitude decreases (22%) as far as Chatham Point, and strong tidal currents occur throughout this reach. Continuing southward to Seymour Narrows, the amplitude increases in a short distance to its original range. A further slight increase is noted at Comox, which represents the Strait of Georgia tide. As shown in the Figure, the tides in Seymour Narrows are intermediate in time, range and character between those of the ocean to the north and those of the Strait of Georgia to the south.

The tidal current floods southward and ebbs northward corresponding in direction to the difference of sea level between the ends of the Strait.

The forms of the sea surface during the flood and ebb phases of the tide cycle are shown in Figure 4. Study of these data shows that the tidal cycles north and south of the Narrows are independent phenomena, and that the discontinuity between them occurs in the vicinity of the Narrows because of the constriction in the channel. The large differences in level constitute the hydraulic head which creates the rapid currents. Similar conditions are associated with

tidal rapids in many parts of the world, but few, if any, demonstrate the phenomena on such a scale.

The nature of this discontinuity between the northern and southern tides is strikingly illustrated in Figure 4 by the form of the sea surface. The maximum flow is associated with the maximum slope of the sea surface in the region of the Narrows, whereas the surface in the approaches is very nearly horizontal.

The figure also illustrates two other phenomena of considerable interest. Towards the end of the ebb flow, the sea surface at both ends of the Strait reaches the same elevation. At this time, the surface at Seymour Narrows is considerably below this level. It might be supposed that water would run into

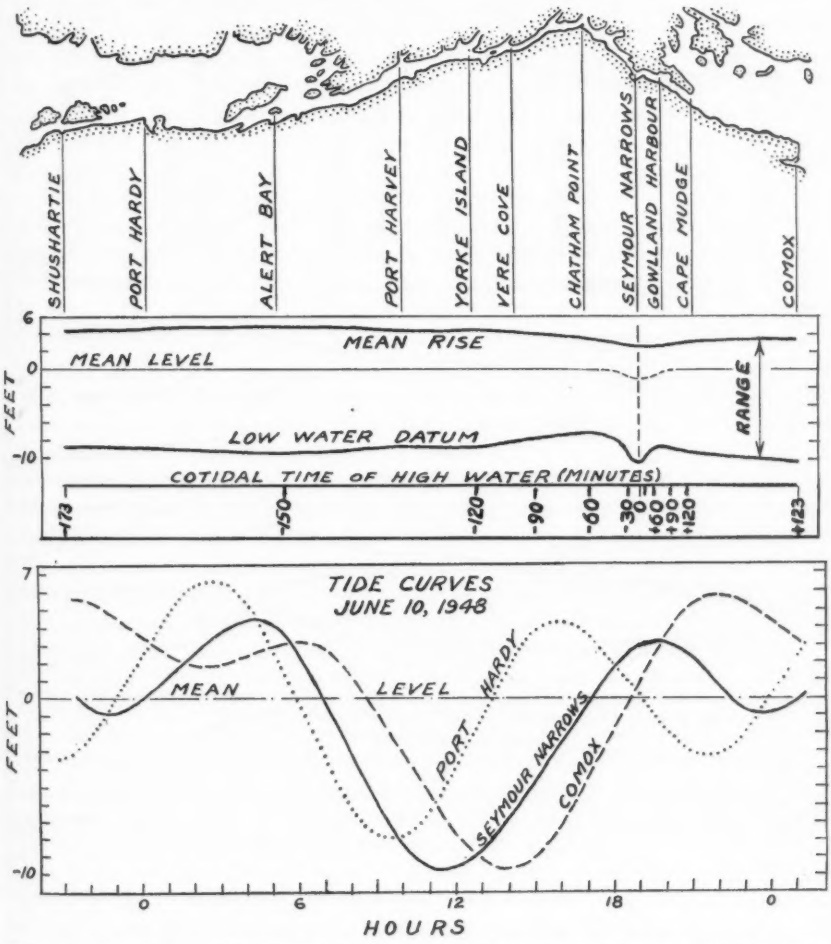

FIGURE 3. Tide curves, and tidal range in Johnstone Strait. From the Tide Tables, 10 June 1948.

the Strait from both ends, and slack water would occur when the opposing currents were equal. Such is not the case. The data (Fig. 4) show that slack water in the Narrows at the end of the ebb flow is associated with a general slope of the sea surface opposing the flow. During the latter part of the ebb the water is running uphill. The converse phenomenon occurs during the flood regime. When the sea surface is at the same level at the ends of the Strait, there is a hump at Seymour Narrows. The water does not run out both ways but continues in the flood direction until opposed by a considerable "ebb" slope.

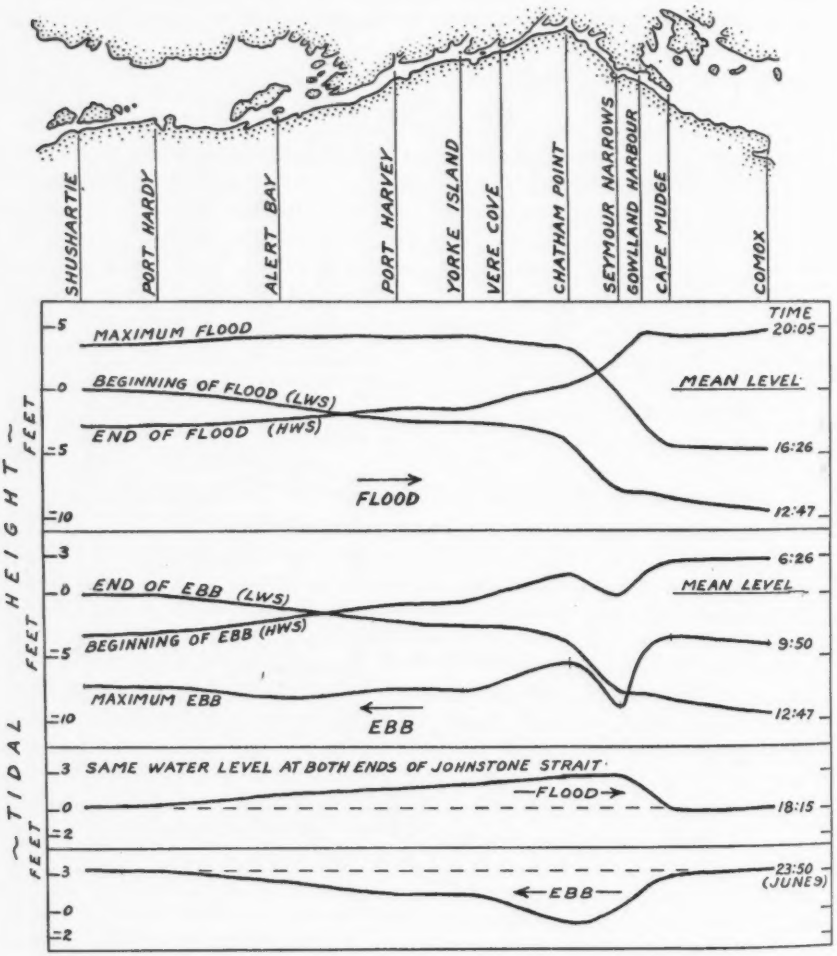

FIGURE 4. Forms of the sea surface in Johnstone Strait at successive tidal stages. From the Tide Tables, 10 June 1948.

The inertia of the moving water mass in Johnstone Strait causes the waning tide to flow for some time after the sea surface becomes horizontal, until the opposing head of the waxing phase becomes great enough to reverse the direction. Thus at the end of the ebb there is a flood potential in Johnstone Strait equal and opposite to the inertia of the ebb flow, and the converse situation occurs at the end of the flood.

It is evident that this is a hydraulic system where the direction and velocity of the current in the Narrows are dependent on the effective difference of sea level between the Narrows and the maximum height upstream. However this latter position is transient along Johnstone Strait and cannot be used for continuous measurement.

The current in Seymour Narrows may be attributed to the head between the Narrows and the nearest point upstream where there is zero velocity. During the flood phase this would require a reference at the northern end of Vancouver Island such as Port Hardy, which is the most reliable tidal station in that vicinity. During the ebb the nearest suitable reference in the Strait of Georgia is at Comox.

The tide curves at these points were shown in Figure 3. The sea level differences between Seymour Narrows and these reference points are shown in Figure 5, along with the corresponding cycle of tidal velocity in the Narrows.

Evidently the flood flow is associated with the positive arch of the Port Hardy curve, and the ebb with the positive arch of the Comox curve. Apart from "backwater" effects, which appear to be small, the velocity and direction of the currents at Seymour Narrows are concerned only with the head above the Narrows. The intersections of the curves mark the times when sea level is the same at both ends of Johnstone Strait. The shaded portions indicate the intervals during which the potential opposes the flow.

Although the ebb flow continues past the time when the opposing heads are equal, it is evident that the flood head commences at this time, and continues until the heads again become equal at a lower level than Seymour Narrows. Therefore, it is reasoned, the flood flow is associated with this arch of the Port Hardy head function. Similarly the ebb head is initiated at this lower equality of the heads, and continues to the completion of the cycle, and the ebb flow is associated with the corresponding arch of the Comox head function.

Owing to the rather large diurnal inequality which is apparent in Figure 5, the duration of a single phase of tidal flow cannot be expected to agree well with the duration of the head, because the flow depends not only on the duration of the preceding and following heads, but also on their rate of change in amplitude. In the four phases shown in the Figure, the differences ranged from 6 to 24 minutes. However, in the complete lunar cycle (1490 minutes) defined by the points of intersection, the total durations of the flow and head should coincide closely, since daily changes in the character of this cycle are relatively small. This is found to be the case.

In the Figure, the total flood head endures for 725 minutes, whereas the flood flow continues for 727 minutes. The ebb head exists for 762 minutes and

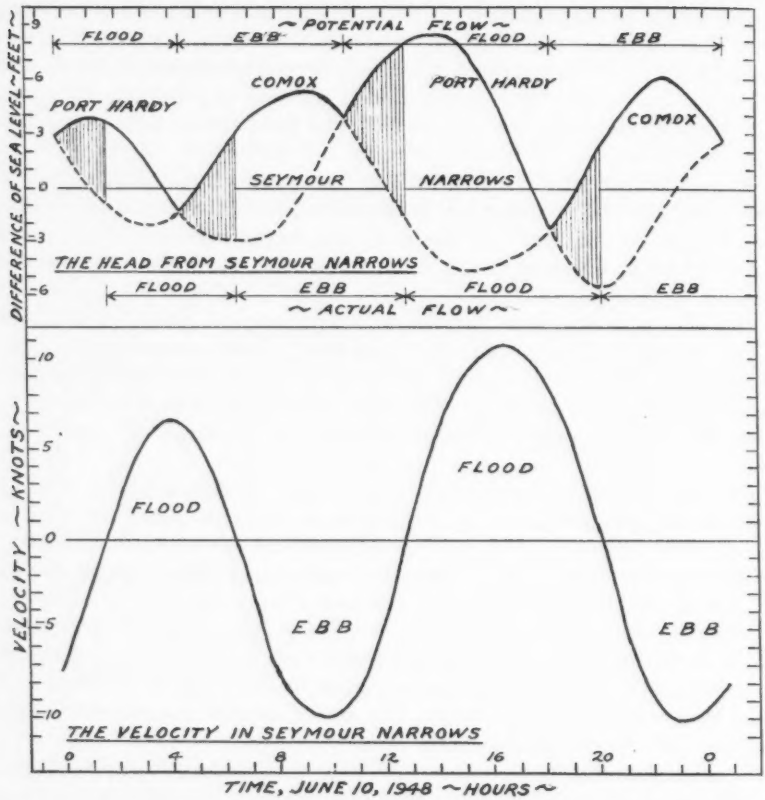

FIGURE 5. The head and velocity functions in Seymour Narrows from the Tide Tables, 10 June 1948.

the flow for 775 minutes. This difference of 13 minutes is less than 2 per cent of the time. When Shushartie, nearer the ocean, was substituted for Port Hardy, the difference decreased to 7 minutes which is less than 1 per cent of the time. This difference could arise from errors made in determining the mean level plane of reference, from errors in the tidal range factors, from time differences in the Tide Tables, which are designed for average conditions, or from a small difference in the friction losses or inertia between the two flows.

The lag from the time of equal heads to the time of slack water is within six minutes of being the same during the two longer phases. The lag between maximum head and maximum flow is quite different (flood 176 minutes, ebb 43 minutes). At the maxima the lag represents the rate of response of the system to a single increasing head which is much farther away on the flood (Port Hardy to Seymour Narrows) than on the ebb (Comox to Seymour Narrows). Evidently

this involves a distance factor. The lag at slack water represents the equality of opposing forces where the distance is not a factor.

OBSERVED SEA LEVELS IN SEYMOUR NARROWS

During the years 1945 to 1950 the Tidal Branch of the Hydrographic Service made exhaustive studies of the tidal rise and the currents in this area, which provided the data for the predictions in the Tide Tables [2] and for determinations of Mean Sea Level at Seymour Narrows and Comox.

Continuous records of sea level (Fig. 6) were obtained with automatic tide gauges at Comox, Bloedel, Brown Bay and Seymour Narrows for periods as shown in Table I. The control level at each station was referred to the Geodetic Datum, and the standard procedures for tide gauging [3] were followed throughout. The mean levels determined by these relatively short series of observations were adjusted to the Geodetic Datum by comparison with the corresponding levels at the primary reference station (Victoria) as demonstrated in Table II.

In Seymour Narrows the form of the tidal height function is appreciably distorted by irregular waves of periods from ten minutes to one hour. These are shown by the water level observations in the Narrows where there is a tendency

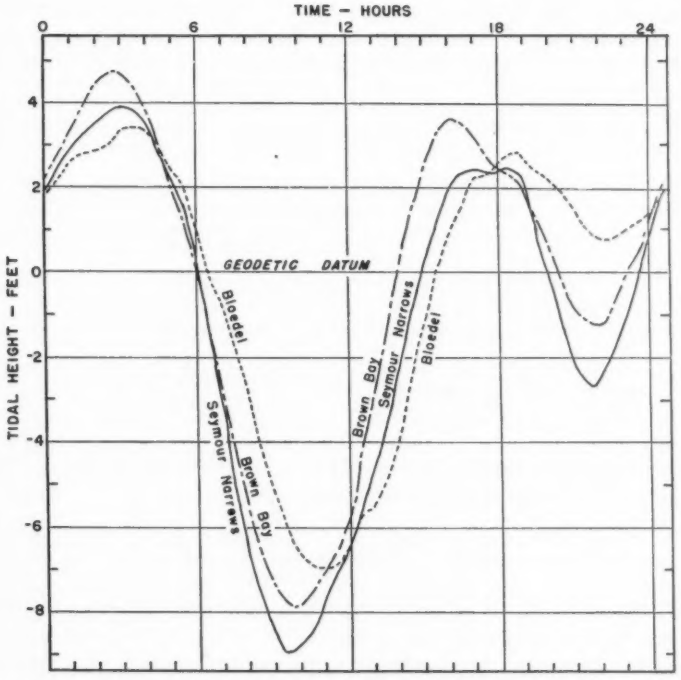

FIGURE 6. Observed cycle of tidal height in Seymour Narrows and vicinity, 26 July 1945.

towards a double high water (Fig. 6). The Canoe Pass data show similar aberrations at low water.

A similar phenomenon at Southhampton, England, has been investigated by Doodson and Warburg [4] who concluded that such effects are not easily assessed.

However, it is likely that these distortions are distributed fairly well over the tidal cycle, and when considering annual averages, the discrepancy which will arise from this effect should be small, and may be neglected.

Mean Sea Level is the mean height of the sea surface (z) at all stages of the tide over a period (T_1 to T_2) of 19 years [3].

TABLE I. Summary of tidal survey observations in the vicinity of Seymour Narrows, B.C.

Maximum current velocities: Seymour Narrows, mid-stream in the fairway east of Ripple Rock, a total of 31 floods and 35 ebbs covering a wide range of velocities, June 8 to September 26, 1945.

Head difference, Canoe Pass Dam: A total of 15 floods and 19 ebbs, simultaneous with velocity observations in Seymour Narrows, July 23 to September 26, 1945.

Water levels: Continuous records, obtained with automatic tide gauges.

	From	*to*
Seymour Narrows (West side Canoe Pass Dam)	May 20/45	May 25/50
Bloedel, Menzies Bay	May 22/45	Dec. 31/45
Brown Bay, Discovery Passage	May 23/45	Jan. 1/46
Canoe Pass (East side Canoe Pass Dam)	Sept. 27/45	Nov. 12/47
Comox, Strait of Georgia	Mar. 29/47	present date

Time of slack water, Seymour Narrows: A total of 50 floods and 48 ebbs, May 24 to July 21, 1945.

Miscellaneous current measurements: On a few days, July 20 to July 28, 1945, scattered current drift observations to outline the pattern of the currents in and around the Narrows.

TABLE II. Example: Adjust Comox mean level of 1949 to the long term mean sea level at Victoria.

Mean level at	Referred to Geodetic Datum
Victoria	−0.142
Comox	−0.092
	Referred to Victoria
Comox	+0.050

Thus, where the Tidal Datum (TD) is an arbitrary plane of reference, the Mean Sea Level (MSL) may be written

$$\text{MSL} = (\text{TD}) + \frac{1}{T_2 - T_1} \int_{T_1}^{T_2} z \, dT. \qquad (1)$$

Normally this is evaluated as the average of hourly observations of sea level over some stated period, usually a year or more.

Geodetic Datum is the standard reference level, and on Vancouver Island it is the mean value of hourly sea level observations throughout a ten-year period

at Victoria [5]. Although differing slightly from Mean Sea Level as subsequently determined over a longer period it has not been adjusted because the permanency of the datum is of considerable importance for engineering works. The Geodetic Datum may be defined as follows:

$$\text{Geodetic Datum} = d + \frac{1}{T_2 - T_1} \int_{T_1}^{T_2} z \, dT, \qquad (2)$$

where d is an arbitrary difference from Mean Sea Level.

In 1929 and 1930 the Geodetic Service extended this reference plane (Geodetic Datum) by precise levelling procedure [5] to Campbell River and Port Alberni. Following an earthquake in 1946, a portion of this work was repeated and the levels extended to Comox, Bloedel, Brown Bay and Canoe Pass on Seymour Narrows [6]. Owing to the difficult terrain, unusual methods were required to reach Canoe Pass, resulting in a possible maximum levelling error of 0.2 feet at this place (private communication).

THE ANOMALY OF MEAN SEA LEVEL

Mean Sea Level varies from the Geodetic Datum in an irregular manner from place to place. Some of these variations have been attributed to variations in gravity [7], others to prevailing winds, but most of them are unexplained.

The differences (d) between the Geodetic Datum and the mean sea levels observed at several positions around Vancouver Island are shown in Table III. Where these differences are small—less than one-tenth of a foot, as at Victoria, Comox and Port Alberni—they are usually accepted without serious question. However, when the difference is greater than two-tenths of a foot it is considered anomalous. Such is the case at Seymour Narrows [8], where the Mean Sea Level is nearly half a foot lower than the Datum and the sea levels at other positions in the region. This anomaly is real because it is considerably greater than the possible error of levelling (0.2 feet).

TABLE III. Differences of adjusted values of annual mean sea level at points around Vancouver Island from the Geodetic Datum established at Victoria. (Values are in feet above (+) or below (−) the datum.)

	Victoria	Comox	Port Alberni	Seymour Narrows[a]
1946	−0.070			−0.505
1947	−0.091			−0.435
1948	+0.007		+0.030	−0.475
1949	−0.142	+0.050	+0.046	−0.448
1950	+0.017	+0.086		
Mean	−0.039	+0.068	+0.038	−0.466

[a]Seymour Narrows, west side of Canoe Pass Dam.

CALCULATION OF THE ANOMALY FROM TIDAL HEIGHT DATA

The Tide Tables [3] list the height and time of successive high and low water referred to an arbitrary local tidal datum [9]. From these data the average

annual values were calculated and referred to the Geodetic Datum as shown in Table IV. A tide curve was fitted to these in the standard manner [10] as shown in Figure 7.

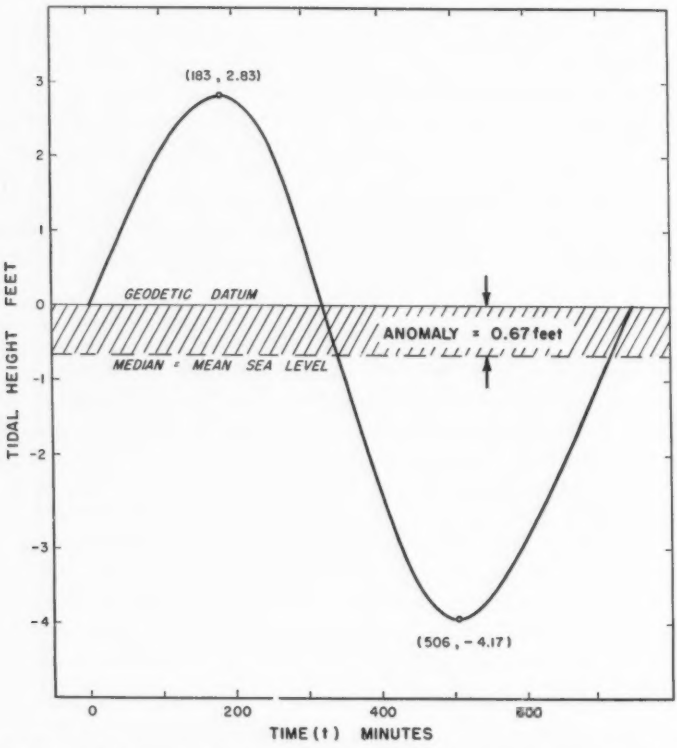

FIGURE 7. The 1948 average tide cycles at Comox and Seymour Narrows, and the average difference of sea level. From the Tide Tables.

This curve is defined solely by the time and height of a single high and low tide, and is interpreted as though the rise and fall were simple sine functions of time. Therefore, the curve is symmetrical about the median axis which is Mean Sea Level. The difference between this and the Datum is the anomaly (Equation 2).

The median (anomaly) of the 1948 average tide cycles is 0.67 feet below the Geodetic Datum, as shown in Table IV. When this is compared with the observed value of –0.475 (Table III) it is realized that the apparent error of 0.2 feet is the same as the maximum possible error of the Geodetic Datum from which the observed value is measured. It is probable that the error is in the calculated value based on the necessary assumption that the average tide curve is symmetrical, whereas the observed value is based on hourly measurements of

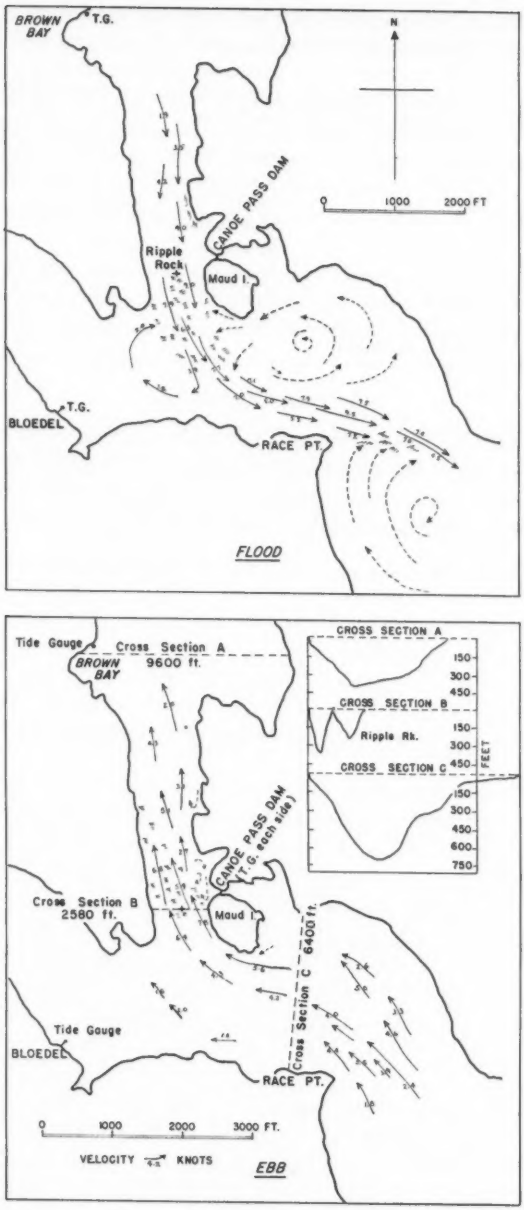

FIGURE 8. Detail of Seymour Narrows showing the course of the tidal streams, August 1945.

tidal height. However, the method of analysis of the tidal data is accepted [10] and the possibility of error in the Datum is real.

TABLE IV. Characteristics of the average tidal height curves at Seymour Narrows, 1948. (From the Tide Tables.)

Average H.W.	height (feet)	2.48
	time (minutes)	211.0
Average L.W.	height (feet)	−4.17
	time (minutes)	534.2
Average cycle	(minutes)	745.2
Average range	(feet)	7.00
Average amplitude	(feet)	3.50
Median (Mean sea level, anomaly)	(feet)	−0.67

THE TIDAL CURRENTS

The course of the tidal stream and the relative velocities in various parts of the channel were observed while the investigators drifted through the Narrows on calm days. These data are summarized in Figure 8 for tides of medium velocity during the strength of the flood and ebb flows.

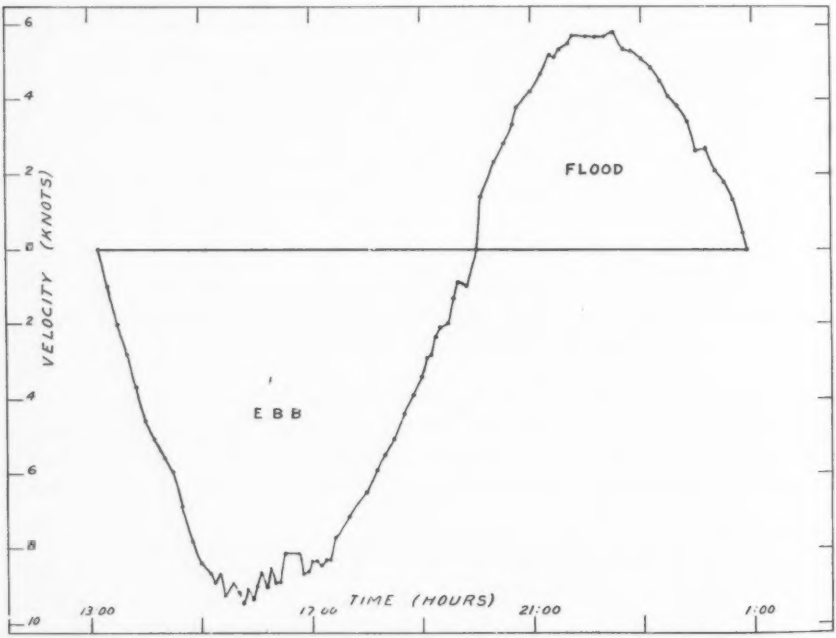

FIGURE 9. A cycle of observed velocities in Seymour Narrows measured at ten minute intervals from a barge anchored near Ripple Rock, 8 October 1943. This is one example of six series of such measurements made by R. P. Henderson, Department of Public Works, Canada.

The only complete cycles of current velocity available were observed by the Dominion Department of Public Works from a barge anchored in midstream near Ripple Rock. Figure 9, which is an example of this cycle, illustrates in considerable detail the character of the smooth curve of Figure 5.

Maximum current velocities (Fig. 10) were observed in the fairway east of Ripple Rock. These observations (Table I) [11] were limited to the time and velocity at the maxima, and the time of slack water. These were sufficient for navigational purposes, consequently there are no long series of data corresponding to Figure 9.

The current was stemmed with a ship of ample power, so that a fixed position was maintained by adjusting speed and helm. Velocities up to 13 knots were measured by streaming a ship's log, previously calibrated, and timing the distance logged.

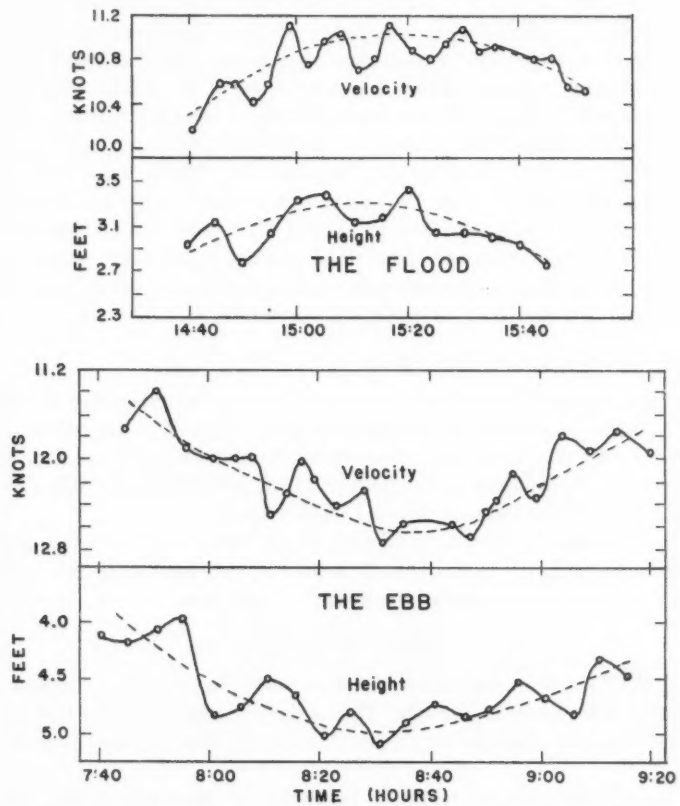

FIGURE 10. Examples of the maximum current velocities in Seymour Narrows, and the maximum head across Canoe Pass Dam. Series of such observations were made as catalogued in Table V.

The measurements contain some inaccuracy resulting from slight movements of the station vessel. However, on each tide many short measurements were taken, the end of one coinciding with the start of the next. Consequently such errors are largely compensating and disappear when the data are smoothed. Surges in velocity with periods ranging from ten to twenty minutes were noted. These are not due to the motion of the ship, but are real, as confirmed by the corresponding oscillations of water level in and around the Narrows. These surges are most intense when the current velocity is high, indicating that they are probably functions of the velocity rather than of wind or barometric pressure differences.

Observed Sea Level Differences

A dam was built across Canoe Pass (Fig. 1, 8) in 1942, to stop the strong current from this channel, which tended to set southbound vessels toward Ripple Rock on ebb tides. There is a difference of water level across this dam which was noticed when establishing a tide gauge nearby. The Seymour Narrows side is the higher during the flood (south-flowing current) and the lower during the ebb (north-flowing current). From the geography it is evident that this head difference must be related to the head difference between sections B and C (Fig. 8). Measurements were made to evaluate, if possible, the relation of this head with the current velocity in the Narrows [12]. These were first made by establishing graduated scales in the water immediately east (Canoe Pass) and west (Seymour Narrows) of the dam so that they were both visible from the observer's station, and were correlated by levelling. A competent man recorded the water levels at five-minute intervals, making each pair of readings within a few seconds, so that they may be considered simultaneous.

The Observed Relation of Tidal Head to Maximum Current

The head across Canoe Pass dam and the current velocities in Seymour Narrows were each plotted as functions of time (Fig. 10). The corresponding surges in velocity and level were eliminated by smoothing by eye [3], and the values of maximum velocity and maximum head difference were taken from the smoothed curves. These data are shown in Table V.

By comparison, as shown in Figure 11, it was found that the maximum head difference (ΔZ_{max}) is a linear function of the square of the maximum velocity (V^2_{max}) having the form of the hydraulic equation,

$$\Delta Z_{max} = kV^2_{max} + C, \tag{3}$$

where k and C are characteristic parameters which have different values during the flood and ebb phases of the tide. This equation, expressing the instantaneous relation between the maxima of the two functions, was evaluated as shown in Table VI.

Automatic tide gauges were in operation at Bloedel, Brown Bay and Seymour Narrows while the current measurements were being made in the Narrows. The water level data from these records were analysed and compared

TABLE V. The observed maximum velocities in Seymour Narrows and the corresponding difference in head across Canoe Pass Dam interpreted from the data as exemplified in Figure 10.

Flood			Ebb		
Date	Velocity	Head	Date	Velocity	Head
1945	*knots*	*ft.*	1945	*knots*	*ft.*
July 28	11.62	3.38	July 23	10.39	3.37
29	9.08	2.37	27	11.10	4.13
			28	10.70	3.77
Sept. 12	6.58	1.19	29	10.38	3.55
13	5.00	0.63			
14	7.86	1.70	Sept. 12	7.82	2.03
15	7.87	1.62	13	6.63	1.50
16	8.29	1.92	14	5.93	1.11
17	9.08	2.13	15	5.80	1.10
18	10.00	2.62	16	6.30	1.42
20	11.48	3.63	17	7.67	1.97
21	11.58	3.82	18	9.20	3.00
22	11.77	3.93	19	10.67	3.86
23	11.53	3.85	20	10.87	3.91
24	11.02	3.32	21	11.87	4.87
26	8.47	1.97	22	12.28	5.22
			23	12.63	5.47
			24	12.46	5.40
			25	11.78	4.63
			26	10.60	3.80

Mean deviation of time of maximum head from time of maximum current: flood: -1 (± 7) min.; ebb: -6 (± 6) min.

TABLE VI. The relation[a] of maximum head between positions in the vicinity of Seymour Narrows to the maximum velocity in the Narrows, with the probable error (P.E.) of the relations.

Canoe Pass to Seymour Narrows	
Flood $\Delta Z_{max} = 0.0285\ V^2_{max} - 0.083$	P.E. $= \pm 0.016$
Ebb $\Delta Z_{max} = -0.0346\ V^2_{max} + 0.062$	P.E. $= \pm 0.017$
Bloedel to Seymour Narrows	
Flood $\Delta Z_{max} = 0.0138\ V^2_{max} - 0.159$	
Ebb $\Delta Z_{max} = -0.0262\ V^2_{max} - 0.147$	
Bloedel and Brown Bay	
Flood $\Delta Z_{max} = 0.0289\ V^2_{max} - 0.145$	
Ebb $\Delta Z_{max} = -0.0185\ V^2_{max} + 0.004$	
Comox and Seymour Narrows	
Flood $\Delta Z_{max} = 0.0479\ V^2_{max} - 0.569$	P.E. $= \pm 0.033$
Ebb $\Delta Z_{max} = 0.0527\ V^2_{max}$	P.E. $= \pm 0.030$

[a]The data (Table I) were plotted as in Figure 11 and the best straight line was fitted by the method of least squares.

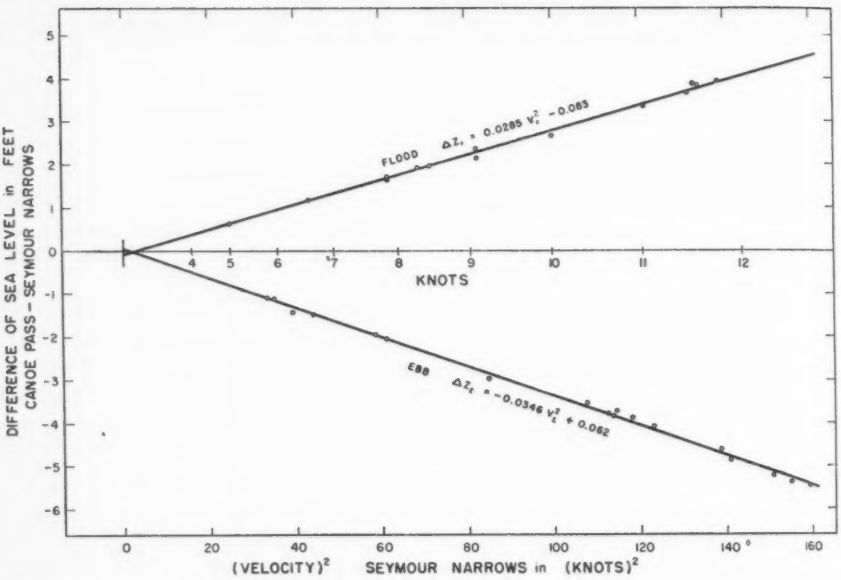
DIFFERENCE OF SEA LEVEL in FEET
CANOE PASS – SEYMOUR NARROWS
FLOOD
$\Delta Z_t = 0.0285\ V_t^2 - 0.063$
KNOTS
EBB
$\Delta Z_t = -0.0346\ V_t^2 + 0.062$
(VELOCITY)² SEYMOUR NARROWS in (KNOTS)²

FIGURE 11. The relation of maximum current velocities in Seymour Narrows to the head across Canoe Pass Dam, from the data in Table V.

in a similar manner with the observed current velocities. The resulting relations are also shown in Table VI. There was considerably more scatter in the data taken from the tide records and this may be attributed to a reading error, to slight defects in the tide recording instruments or, more likely, to real variations in the relations.

The differences in sea level between Seymour Narrows and Comox were not observed simultaneously with the current observations so direct comparisons could not be made in this case. However, comparison of the available measurements, as shown in Figure 12, proved that the head from Comox to Seymour Narrows was proportional to the head across Canoe Pass Dam. This permitted the calculation of the hydraulic relations referred to Comox, as shown in Table VI.

From these and similar analyses it was concluded that the head maxima between any pairs of reference points in the system are proportional.

THE PROBABLE ERROR

The probable error of these relations is shown in the Table VII and indicates that the precision of the Canoe Pass relation is good, but the reliability becomes less with the separation of the head measurement stations. Much of this variability must be due to uncertainty in the interpretation of the irregular maximum velocity data (Fig. 10). These data were smoothed by eye, and it is quite likely

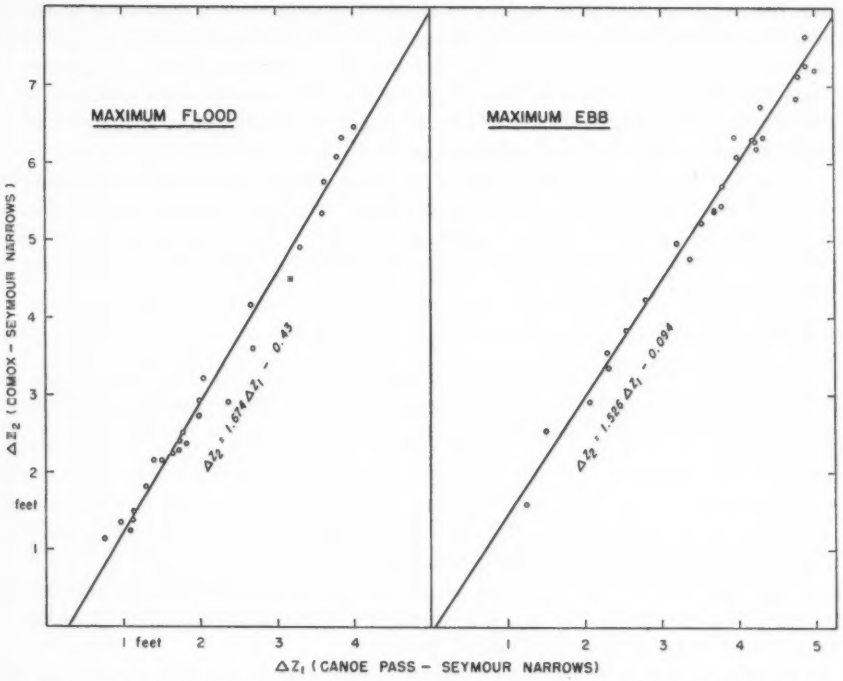
MAXIMUM FLOOD
MAXIMUM EBB
ΔZ2 (COMOX – SEYMOUR NARROWS)
feet
ΔZ1 (CANOE PASS – SEYMOUR NARROWS)
ΔZ2 = 1.674 ΔZ1 – 0.43
ΔZ2 = 1.526 ΔZ1 – 0.094

FIGURE 12. Relation of the head from Comox to Seymour Narrows to the head across Canoe Pass Dam.

TABLE VII. Characteristics of the average annual head cycles (1948) in Johnstone Strait, B.C. (From data in the Tide Tables [3].)

Port Hardy to Seymour Narrows		Comox to Seymour Narrows	
Time	Height	Time	Height
minutes	*ft.*	*minutes*	*ft.*
211	0	297	2.83
297	2.83	373	0
436	**4.94** (H_{Fmax})	525	−3.20
628	0	662	−1.48
662	−1.48	710	0
793	−4.00	917	**5.20** ($H_{E\,max}$)
957	0	1042	2.83
1042	2.83	1118	0

that the resulting values of head and velocity are not strictly consistent in each instance, although it is presumed that such errors are random in the derivation of the velocity head relations. Also the sea level differences were interpreted from the recorded tide curves at Seymour Narrows and Comox, whereas the differences across Canoe Pass Dam were observed directly, so it is likely that a reading error is also included in these data.

The current velocities published in the Tide Tables [2] are predicted by the British Tidal Institute and are based on these maximum velocity observations. Therefore the probable error of these predictions may be assumed to be 0.6 knots, and it is calculated that 5% of the velocities may differ more than 2 knots from the predicted values.

The Hydraulic Equation

Although the form of Equation 3 suggests the hydraulic equation, it has a number of significant differences. In its simplest form the hydraulic equation is synonymous with the Torricelli Equation representing the steady flow of a perfect fluid:

$$\Delta Z = \frac{V^2 - V_0^2}{2g} = \frac{V^2}{2g} - \frac{V_0^2}{2g},$$

where V_0 is the initial velocity and g is gravity.

The flow in Seymour Narrows is continually accelerating in one direction or the other, except at the maxima when the acceleration vanishes. Thus the condition of steady flow is fulfilled in Equation 3.

In any natural flow there is a loss of energy due to viscosity, friction and turbulence which are not considered in the simple equation. This has been studied by many workers, notably Prandtl, Taylor and von Karman, on the basis of shear stresses [13].

This cannot be applied to the present case since there are no measurements of the velocity gradient and from casual observation it appears to be negligible. The only gradients appear to be between the centre and periphery of the individual eddies, and are not readily measured. However dynamical similarity indicates and experiment confirms [13] that all these losses can be expressed as head losses in terms of the average velocity head. This may be closely approximated by

$$\text{Friction loss} = \frac{2F}{2g}\left(\frac{V^2 + V_0^2}{2}\right)$$

where F incorporates the coefficient of turbulent friction and the hydraulic dimensions, and may be considered as a constant characteristic of the system.

Setting this in the Torricelli Equation:

$$\Delta Z = \frac{V^2}{2g}(1+F) - \frac{V_0^2}{2g}(1-F). \tag{4}$$

This is a completely general expression for the relation of head to average current velocity in any system of steady flow and constant surface pressure. This

equation is identical in form, but not necessarily in meaning with Equation 3 and the observed relations in Table VI, because the head and velocity are interdependent in only two of these.

It is true for the ebb relation between the ebb velocity and the head from Canoe Pass Dam to Seymour Narrows. It may be assumed that the water level above the dam is the same as that in the stream opposite the Pass, south of Maude Island (Fig. 8, Section C). In this case

$$k \equiv \frac{1+F}{2g}\,; \quad -C \equiv \frac{V_0^2}{2g}(1-F).$$

It may also be assumed that the head from Seymour Narrows to Comox is related to the velocity in this form, although it should be noted that the initial velocity is negligible at Comox whence $V_0^2 = 0$ and the constant term (C) vanishes.

During the flood these heads are measured downstream from the velocity measurement and cannot be related to it in terms of Equation 4. Bloedel and Brown Bay are in back eddies on the opposite side of the stream and are not strictly comparable to the flow in Seymour Narrows. However it is evident from the consistent form of the relations in Table VI and consideration of the meaning of Equation 4 that any two hydraulic systems (1 and 2) must be related whether they are continuous or not.

Consider two hydraulic systems

$$\Delta Z_1 = k_1 V_1^2 + C_1 \tag{5a}$$

and

$$\Delta Z_2 = k_2 V_2^2 + C_2, \tag{5b}$$

where the constants k and C have the significance assigned in Equation 4. Then the ratio of the heads and the velocities may be expressed by

$$\frac{\Delta Z_2 - C_2}{\Delta Z_1 - C_1} = \frac{k_2 V_2^2}{k_1 V_1^2},$$

from which one velocity can be expressed in terms of the other:

$$k_2 V_2^2 = \frac{\Delta Z_2 - C_2}{\Delta Z_1 - C_1} k_1 V_1^2.$$

Setting this in the second relation above (Equation 5b)

$$\Delta Z_2 = \left(\frac{\Delta Z_2 - C_2}{\Delta Z_1 - C_1} k_1\right) V_1^2 + C_2. \tag{6}$$

This expression has the form of Equation 5 but relates the head in one system to the velocity in another. By this relation the ebb heads in Table VII could be related to the flood velocities and vice versa.

In the case where two heads are related to one velocity ($V_1^2 = V_2^2$) the relation of the heads becomes

$$\Delta Z_2 = \frac{k_2}{k_1} \Delta Z_1 + \left(C_2 - \frac{k_2}{k_1} C_1 \right), \tag{7}$$

which also has the form of Equation 5 but still does not specify that the heads be in the same hydraulic system. Evidently the heads measured below Seymour Narrows, and the heads from Bloedel and Brown Bay are related to the velocity in this manner.

The fourth case arises when the initial velocity at one of the upper reference points is zero ($C_2 = O$). Then

$$\Delta Z_2 = \frac{k_2}{k_1} (\Delta Z_1 - C_1) \tag{8a}$$

and substituting from Equation 6

$$\Delta Z_2 = \frac{1+F_2}{1+F_1} \Delta Z_1 - \frac{(V_0^2)_1}{2g}(1-F_1). \tag{8b}$$

This is identical with the relation of the ebb heads from Seymour Narrows to Canoe Pass (ΔZ_1) and from Seymour Narrows to Comox (ΔZ_2) as shown in Figure 11. The equation takes the form shown in Table VII by substituting from Equation 5a in Equation 8a:

$$\Delta Z_2 = \frac{k_2}{k_1} (k_1 V_1^2). \tag{9}$$

The correspondence of the observed data with this relation is conclusive proof that the initial velocity (V_0) at Comox may be assumed to be zero.

Cause of the Anomaly

The hydraulic equation requires that the depression of the sea surface be proportional to the square of the velocity. When the velocity increases, owing to constriction of the channel, the head must also increase. This is accomplished by an accumulation of water above the Narrows as shown in Figure 4. However the level of this accumulation is limited by the source of the water in the northern ocean during the flood, and in Georgia Strait during the ebb. Since these levels cannot be raised, the level in Seymour Narrows must be depressed.

The fastest currents occur in the most constricted part of the Narrows, a few hundred feet south of the position where the water observations were made. In accord with Equation 4, the sea surface must be lowest at this position of maximum current, and is somewhat higher at positions upstream and downstream.

If it is assumed that the energy loss is the same at any section, and that the discharge and depth are constant, the form of the various possible surface profiles can be calculated. The form resulting for a constricted channel is illustrated in Figure 13 where the flood is shown flowing from left to right and the ebb in the opposite direction. Since a constant energy loss has been presumed, the depression of the surface which appears can only be due to the velocity

increase in accord with the hydraulic relation. Therefore the Anomaly of Mean Sea Level is the mean value of all the head losses due to the velocity increase associated with the constriction of the channel.

Similar head losses are always associated with rapid currents in seaways, consequently, with the possible exception of very shallow channels where the critical depth may affect the situation, a corresponding anomaly is to be anticipated in every case.

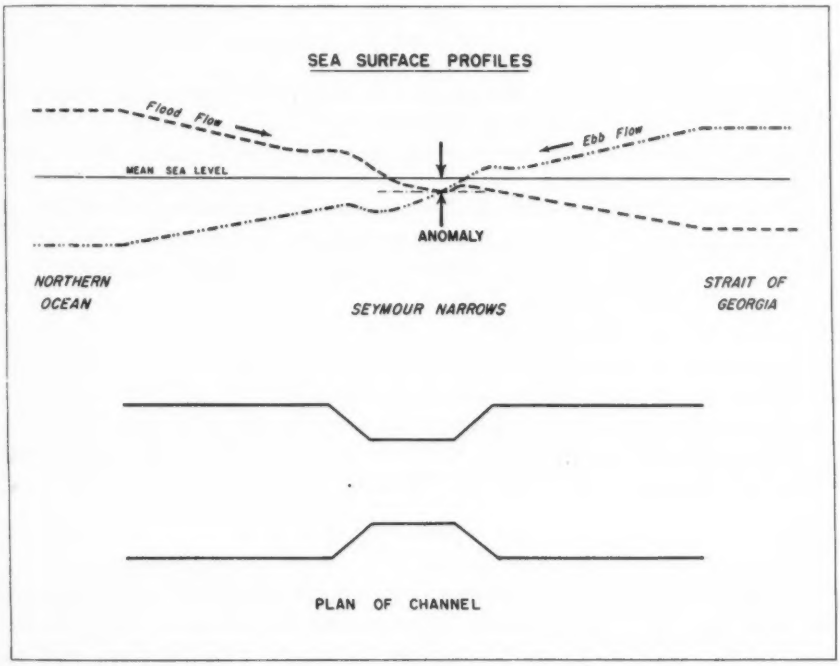

FIGURE 13. The form of the water surface, assuming steady flow between constant level reservoirs in a constricted channel, and energy loss the same as in uniform flow at the same discharge and depth.

CALCULATION OF THE ANOMALY FROM TIDAL CURRENT DATA

The anomaly may be expressed as the difference in mean sea level (ΔZ) between an accepted reference position (Z_0) such as Comox, and an observation point (Z_1) such as Seymour Narrows.

$$\text{Anomaly} = d + \frac{1}{T_2 - T_1} \int_{T_1}^{T_2} (Z_0 - Z_1) dT, \qquad (10)$$

where d is the difference of the Geodetic Datum from Mean Sea Level at the point of reference.

It is evident that by suitable choice of reference stations during the flood and ebb flow, the head (ΔZ) in the hydraulic equation may be identified with the difference of sea level in this definition of the anomaly. Therefore the anomaly may be determined from the velocity function alone, when it is expressed as a function of time,

$$\Delta Z = kV^2 + C = kV^2_{max}\phi(t) + C,$$

and, substituted into the equation,

$$\text{Anomaly} = d + \frac{kV^2_{max}}{\Delta t}\int_0^{\Delta t}\phi(t)dt + C.$$

It is convenient to solve this problem in three steps; first find the most suitable head-velocity relation, then determine the form of the average velocity cycle, then substitute this into the equation and determine the mean value defined by the integral term.

The constant (C) is eliminated when the relation involves the total head (H) as in the relation of the head between Seymour Narrows and Comox, to the maximum velocity at Seymour Narrows (Table VI) which is assumed to represent the annual average relation

$$H_{Emax} = 0.0527\overline{V^2}_{Emax}. \tag{11}$$

There are no corresponding data to the northward for the flood head (H_F). However it has been noted that the velocities in the vicinity of Port Hardy are small, and may be considered negligible in the same sense as those at Comox. Then from Equation 9 the relation may be written

$$H_{Fmax} = \frac{k_{F_2}}{k_{F_1}}(0.0479\overline{V^2}_{Fmax})$$

where $H_{F\,max}$ is the head from Seymour Narrows to Port Hardy associated with the maximum flood flow, k_{F_2} is the unknown constant (k) associated with this head-velocity relation; k_{F_1} is the constant associated with the flood relation referred to Comox (0.0479) from Table VI. The equation may be evaluated from the tidal data at Comox, Port Hardy, and Seymour Narrows. The average annual tide curves were evaluated, and the average head curves were drawn. From these the characteristic values in Table VII were determined:

$$\frac{k_F}{k_E} = \frac{H_F}{H_E} = \frac{\Delta Z_{Fmax}}{\Delta Z_{Emax}} = \frac{4.94}{5.20} = 0.950.$$

Then the flood relation referred to Port Hardy is

$$H_{Fmax} = 0.0455\overline{V^2}_{Fmax}. \tag{12}$$

The data in the tidal current tables define the time of slack water and the time and velocity of the maxima. From these data the average annual characteristics were calculated for 1948 and 1949 as shown in Table VIII.

TABLE VIII. Characteristics of the average annual velocity cycle in Seymour Narrows. (From the Tide Tables.)

	1948	1949
Maximum flood velocity (*knots*)	8.49	8.47
Squared function ($\overline{V}^2_{F\,max}$)	75.41	75.00
Duration of flood ($t_2 - t_0$) (*minutes*)	369.7	368.0
Difference (d_F) MSL Port Hardy from Geodetic Datum, assumed same as Alberni (Table III)	0.030	0.046
Maximum ebb velocity (*knots*)	−9.70	−9.64
Squared function ($\overline{V}^2_{E\,max}$)	96.91	96.08
Duration of ebb ($t_4 - t_2$) (*minutes*)	375.6	376.6
Difference (d_E) MSL Comox from Geodetic Datum	[a](0.053)	0.050
Duration of average cycle ($t_4 - t_0$) (*minutes*)	745.3	744.7

Flood relation referred to Port Hardy: $H_{F\,max} = 0.0455\ \overline{V}^2_{F\,max}$ (12)

Ebb relation referred to Comox: $H_{E\,max} = 0.0527\ \overline{V}^2_{E\,max}$ (11)

[a]Assumed proportional to observed anomaly at Seymour Narrows (Table III).

There is some question regarding the form of the velocity-time function. The literature [7, 14] favours a relation of the form

$$\overline{V} = V_0 + A\sin(\omega t+\alpha) + B\sin(\omega t+\beta) + \ldots$$

whence the square of the velocity would be a complex function involving squares and cross products.

If this type of relation is accepted a very simple and close approximation to the data in Table VIII can be made by assuming that each quadrant of the velocity squared-time function is of the form

$$\overline{V}^2 = \overline{V}^2_{max}\sin^2\omega t \qquad (13)$$

with the angular velocity w adjusted to suit the time interval, as illustrated in Figure 14. Then the definition of the anomaly becomes:

$$\begin{aligned}\text{Anomaly} = &-\frac{d_F}{2} + \frac{t_1-t_0}{t_4-t_0}\cdot\frac{k_F\overline{V}^2_{Fmax}}{t_1-t_0}\int_{t_0}^{t_1}\sin^2\omega t\,dt \\ &+\frac{t_2-t_1}{t_4-t_0}\cdot\frac{k_F\overline{V}^2_{Fmax}}{t_2-t_1}\int_{t_1}^{t_2}\sin^2\left(\frac{t_1-t_0}{t_2-t_1}\right)\omega t\,dt \\ &-\frac{d_E}{2} + \frac{t_3-t_2}{t_4-t_0}\cdot\frac{k_E\overline{V}^2_{Emax}}{t_3-t_2}\int_{t_2}^{t_3}\sin^2\left(\frac{t_1-t_0}{t_3-t_2}\right)\omega t\,dt \\ &+\frac{t_4-t_3}{t_4-t_0}\cdot\frac{k_E\overline{V}^2_{Emax}}{t_4-t_3}\int_{t_3}^{t_4}\sin^2\left(\frac{t_1-t_0}{t_4-t_3}\right)\omega t\,dt.\end{aligned}$$

The difference d_F of mean sea level at Comox from the Geodetic Datum (Table III) was not observed in 1948, and since other evidence was lacking it was assumed to be proportional to the 1949 value in the same ratio as the observed anomaly at Seymour Narrows. The difference (d_E) at Port Hardy was

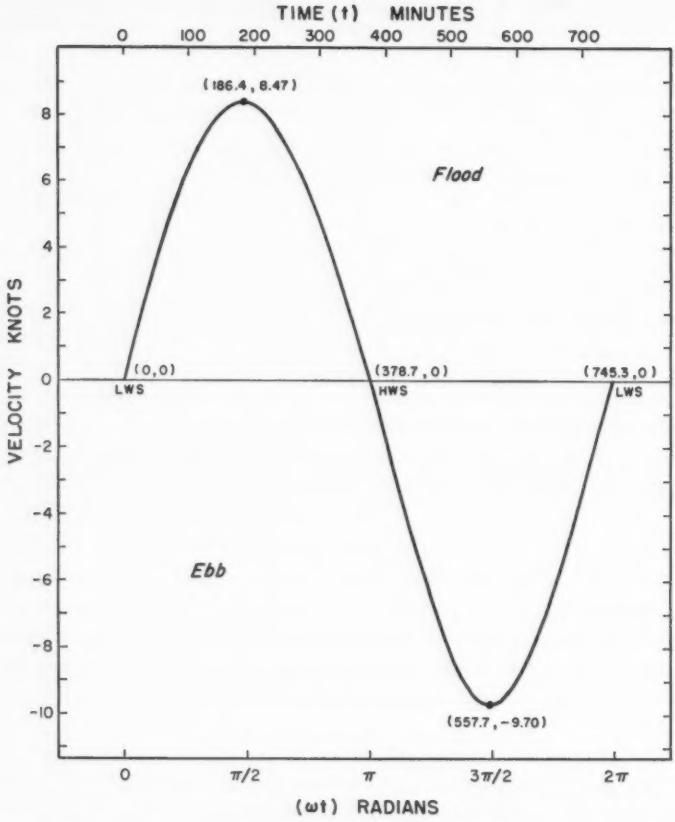

FIGURE 14. The 1948 average velocity cycle in Seymour Narrows from the Tide Tables.

assumed to be the same as at Alberni, which is also on the ocean coast. Since both of these values are small and the time proportions are nearly equal, the difference terms may be combined and approximated by

$$\frac{d_F(t_2-t_0)+d_E(t_4-t_2)}{t_4-t_0} \approx \frac{d_F+d_E}{2}.$$

Then the anomaly reduces to

$$\text{Anomaly} = -\frac{d_F+d_E}{2}+\frac{[(t_2-t_0)k\overline{V^2_{max}}]_F+[(t_4-t_2)k\overline{V^2_{max}}]}{2(t_4-t_0)} \qquad (14)$$

which may be solved from the data shown in Table VIII. The second term is the difference of Mean Sea Level at Seymour Narrows from that of the reference stations, while the whole quantity is the anomaly from the Geodetic Datum.

The calculated values shown in Table IX are slightly less than the observed anomalies in 1948 and 1949, within very small limits, and well within the possible error of the Datum (0.2 feet).

The same literature [7, 14] demonstrates that the head-time relation is a sine function. When this is set in the hydraulic equation it becomes apparent that the velocity-time function should be of the form

$$V = V_0 + A \sin^{\frac{1}{2}}(\omega t + \alpha) + B \sin^{\frac{1}{2}}(\omega t + \beta) + \ldots$$

which would also become very complex. The simplest approximation based on this concept is that each quadrant of the velocity squared-time function is of the form

$$V^2 = V^2_{max} \sin \omega t \tag{15}$$

with the angular velocity (w) adjusted to suit the time interval of each quadrant. This may be set into the definition of the anomaly as in the previous example and solved to show that

$$\text{Anomaly} = -\frac{d_F + d_E}{2} + \frac{2}{\pi} \frac{[(t_2 - t_0)k\overline{V^2_{max}}]_F + [(t_4 - t_2)k\overline{V^2_{max}}]_E}{(t_4 - t_0)} \tag{16}$$

which may be solved from the data in Table IX.

TABLE IX. The anomaly of mean sea level at Seymour Narrows calculated from the data in the Tidal Current Tables [3].

	1948	1949
	ft.	*ft.*
Observed anomaly[a]	−0.475	−0.448
Difference of mean sea level (reference to Seymour Narrows) (MSL—Datum) = $\frac{d_F + d_E}{2}$	−0.436 0.042	−0.437 0.048
Anomaly (Seymour Narrows)	−0.394	−0.389
Apparent error[b]	0.081	0.059
Difference of mean sea level (reference to Seymour Narrows) (MSL—Datum) = $\frac{d_F + d_E}{2}$	−0.555 0.042	−0.557 0.048
Anomaly (Seymour Narrows)	−0.513	−0.509
Apparent error	−0.038	−0.061

[a]Calculation based on the assumed velocity function $\overline{V^2} = \overline{V^2_{max}} \sin^2 \omega t$ (16)

[b]Calculation based on the assumed velocity function $\overline{V^2} = \overline{V^2_{max}} \sin \omega t$ (18)

The conclusions from this calculation are also shown in Table IX. They are larger than those from the previous assumption by the factor

$$\frac{4}{\pi} = 1.273.$$

They are slightly greater than the observed anomaly, but still within the suggested error of the Datum.

Error

These evaluations of the Anomaly of Mean Sea Level in Seymour Narrows are limited by the accuracy of the definition of the average velocity function (Equations 13 and 15). The differences of the two approximations from the observed anomaly, and from each other, are not sufficient to decide whether Equation 13 or 15 is the more accurate representation.

The conclusions are also limited by the accuracy of the determination of the maximum velocity ($\overline{V}^2_{max}$) and the duration (Δt) of the tidal phases in the average cycle. These values (Table IX) derived from the Tidal Current Tables may be in error by as much as 0.1 knots, and one minute of time. Such discrepancies allow a variation of 0.08 feet in the calculated anomaly.

The observed values are based on actual water elevations which take into account the irregularities of the tide curves (Fig. 6) and are affected by weather conditions.

It is probable that there are residual errors in both the observed and the calculated anomalies. However, until it can be proved otherwise, the observed anomaly is assumed correct, and the error in the calculated anomaly is a fair definition of the limit of accuracy of the method.

Form of Mean Sea Level

The differences of Mean Sea Level from Seymour Narrows to the neighbouring positions were calculated by setting the observed head-velocity relations

Table X. Calculated differences of mean sea level between positions in the vicinity of Seymour Narrows.

	1948	1949
	ft.	*ft.*
Canoe Pass to Seymour Narrows	−0.271	−0.276
Bloedel to Seymour Narrows	−0.501	−0.503
Bloedel and Brown Bay	+0.052	+0.051
Brown Bay to Seymour Narrows	−0.553	−0.554

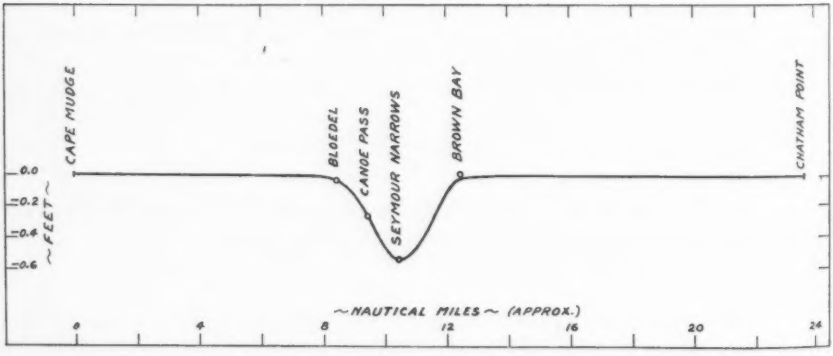

Figure 15. Probable form of Mean Sea Level in the vicinity of Seymour Narrows, as calculated from the relations in Table V.

from Table VI into Equation 8. These results are shown in Table X and the probable form of Mean Sea Level in the region is shown in Figure 15. This confirms the reasoning of Figure 13 where the form of Mean Sea Level was deducted from energy considerations alone. Evidently the Anomaly of Mean Sea Level is real, and is a consequence of the tidal currents in the vicinity.

TRANSPORT AND DISCHARGE

As shown in Table VIII and Figure 14 the average ebb flow endures longer, and the maximum velocity is more than a knot greater, than the flood. Evidently more water flows northward through Seymour Narrows during the ebb than is returned on the flood, so that the net transport is seaward.

This may be expressed

$$\text{Net transport} = B\int_{t_0}^{t_2}\overline{V}_F\,dt - B\int_{t_2}^{t_4}\overline{V}_E\,dt \qquad (17)$$

where B is the area of the cross-section (B in Fig. 8) of Seymour Narrows, and $\overline{V}$ is the average velocity function. If this is assumed to be of the form of Equation 13, the expression becomes:

$$\begin{aligned}\text{Net transport} = {} & B\overline{V}_{F\max}\int_{t_0}^{t_1}\sin\omega t\,dt \\ & + B\overline{V}_{F\max}\frac{t_2-t_1}{t_1-t_0}\int_{t_1}^{t_2}\sin\omega t\,dt \\ & + B\overline{V}_{E\max}\frac{t_3-t_2}{t_1-t_0}\int_{t_2}^{t_3}\sin\omega t\,dt \\ & + B\overline{V}_{E\max}\frac{t_4-t_3}{t_1-t_0}\int_{t_3}^{t_4}\sin\omega t\,dt,\end{aligned}$$

which reduces to:

$$\text{Net transport} = \frac{2}{\pi}B\left[\overline{V}_{F\max}(t_2-t_0)+\overline{V}_{E\max}(t_4-t_2)\right]. \qquad (18)$$

The appropriate values were substituted from Table VIII and the net transport determined as shown in Table XI. In general the ebb exceeds the flood by 7% to 9%.

It was thought that the ebb bias might be associated with total land drainage into the Strait of Georgia, which is about 1.2 times the Fraser River discharge. However the ebb bias in Seymour Narrows is four to five times as great as the drainage, so it must be assumed to be independent of it. The excess ebb discharge through Seymour Narrows must be compensated by an excess flood through the other passages opening to the sea.

CONCLUSIONS

The discussions have shown that Mean Sea Level is depressed in the presence of hydraulic tidal currents wherever the channel exceeds the critical depth. This anomaly may be calculated with considerable accuracy from data

TABLE XI. The necessary factors and calculated transport, discharge, and residual velocity through Seymour Narrows.

Dimensions of cross-section B (*sq. ft.*) in Figure 8	3.86×10^8	
	1948	1949
Velocity, average maximum:		
Flood ($\bar{V}_{F\ max}$) (*ft./sec.*)	14.34	14.30
Ebb ($\bar{V}_{E\ max}$)	−16.40	−16.29
Duration, average tide:		
Flood (*min.*)	369.7	368.0
Ebb	375.6	376.6
Transport in average tide cycle:		
Flood (*cu. ft.* $\times 10^{-10}$)	7.817	7.759
Ebb	−9.082	−9.045
Net	−1.266	−1.286
Discharge (*c.f.s.*):		
Mean rate ($\times 10^{-5}$)	−5.705	−5.826
Land drainage into Georgia Strait (*c.f.s.*) (1.2 × Fraser River discharge):		
Mean rate ($\times 10^{-5}$)	1.365	1.036
Residual velocity:		
Mean rate (*ft./sec.*)	1.478	1.509
(*knots*)	0.875	0.891

defining the maxima of the tidal height at the site of the anomaly and at a reference station. It may also be calculated from knowledge of the velocity maxima or, lacking these, from a knowledge of the velocity-head relation in the seaway.

ESTABLISHMENT OF MEAN SEA LEVEL

It is evident from this study that tidal stations intended to produce the best value of Mean Sea Level on which to base the Geodetic Datum, or to check an extended net of precise levels, should not be located in a seaway where appreciable currents exist.

It follows that the Mean Sea Level at Victoria, which is located on Juan de Fuca Strait where there are considerable currents, must be somewhat lower than in the open ocean, or in the Strait of Georgia. This conclusion is supported by the Mean Sea Level values established from observations at Comox and Port Alberni (Table III) both of which are about half an inch higher than Victoria. However, the evidence is inconclusive in this case because the anomaly is nearly the same as the admitted probable error of the precise levels on which it is based.

Although the anomaly in Seymour Narrows has been shown to exceed all the probable errors of observation and levelling, nevertheless it should be noted that the values determined here depend on the published Geodetic levelling results. Nothing in this study affords a means of assessing the probable levelling error at Canoe Pass, which may be appreciable, and confirmation of this must await further work by the Geodetic Service.

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Notes on the Geographical Distribution and the Hosts of the Cestode Genus *Triaenophorus* in North America[1]

By G. H. Lawler[2] and W. B. Scott[3]

ABSTRACT

The known range of the genus *Triaenophorus* in North America lies between 42°N. latitude (Indiana, U.S.A.), northward to 67°N. latitude (Great Bear Lake, Northwest Territories, Canada), and from the lower St. Lawrence River northwesterly to Alaska. The southern limit of distribution of the genus appears to be closely related to the 70° July isotherm. An hypothesis of the origin and dispersal of the genus is given. From published records and personal communications, the genus is reported to occur in 32 species of fish.

INTRODUCTION

Cestodes of the genus *Triaenophorus* have been known in the Old World since the establishment of the genus by Rudolphi in 1793. The genus is distributed throughout the Holarctic regions of the world and is represented by three species, *T. crassus* Forel, *T. nodulosus* (Pallas) and *T. stizostedionis* Miller. Although all three species are found in North America,[4] only the first two species are known to occur in Europe.

The cestodes *T. crassus* and *T. nodulosus* attain maturity in the intestine of the pike, *Esox lucius*, while *T. stizostedionis* has been found to mature in the yellow walleye, *Stizostedion vitreum vitreum*. The larval stages occur first in a small copepod and later become encysted in the musculature, liver and/or other visceral parts of several fishes.

Investigations of the life histories of members of the genus *Triaenophorus* in Western Canada in recent years have shown that *T. crassus* encysts only in salmonid fishes with the adult stage occurring in the pike. *T. stizostedionis* is not readily distinguishable from *T. nodulosus* to an investigator not completely familiar with members of the genus. Thus, it seems probable that some of the parasites from various hosts reported herein may not have been correctly identified, especially those infected with *T. crassus*, which seems to exhibit a fairly high degree of host specificity.

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[4]*T. crassus* Forel has been variously referred to by North American workers as *T. robustus* Olsson, *T. tricuspidatus* and *T. tricuspidatus* morpha *megadentatus*; while *T. nodulosus* (Pallas) has been referred to as *T. tricuspidatus* Bloch and *T. tricuspidatus* morpha *microdentatus*.

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NORTH AMERICAN DISTRIBUTION

The available records for the North American distribution of the species of *Triaenophorus* are shown in Tables I (Canada) and II (United States). In addition, letters were sent in 1951 and 1952 to various state agencies and personnel, requesting any available records on the distribution of the genus. The results of these enquiries are tabulated in Table III. The various fish species which have been found to harbour the *Triaenophorus* parasite are shown in Table IV.

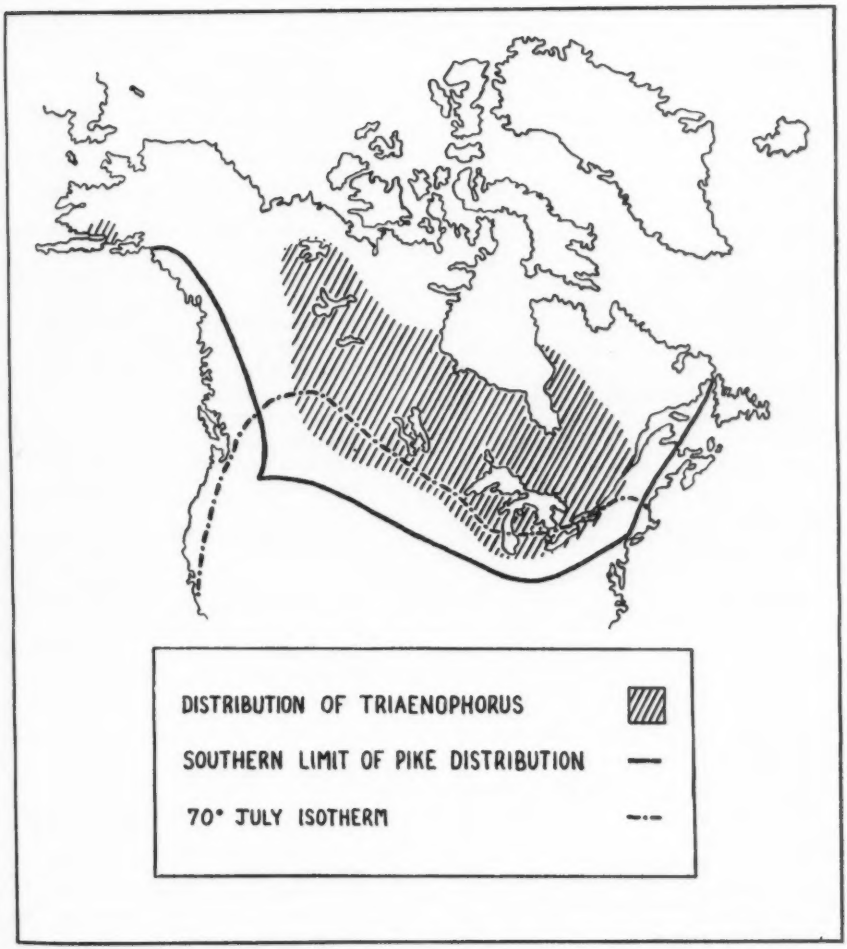

FIGURE 1. Outline map of northern North America showing the principal known distribution of the genus *Triaenophorus*, the 70° July isotherm, and the southern limits of the range of the pike, *Esox lucius*. A record of *T. crassus* from Teslin Lake, B.C., not shown above, suggests a continuous distribution from the Mackenzie drainage to Alaska.

TABLE I. Canadian records of occurrence of genus *Triaenophorus*.

Place	Species of *Triaenophorus*				Fish species infected	Authority
	spp.	*stizosted-ionis*	*crassus*	*nodulosus*		
Quebec						
Western sector of St. Lawrence watershed	...	...	...	x	*Esox masquinongy*	Choquette, 1951
Ontario						
Muskoka District and Georgian Bay	...	...	x	...	*Esox lucius*	Cooper, 1918
	...	...	x	...	*"Lota maculosa"*	
	...	...	...	x	*Micropterus dolomieui*	
	...	...	...	x	*Catostomus commersoni*	
	...	...	...	x	*S. vitreum*	
	...	...	...	x	*Esox masquinongy*	
St. Lawrence River	...	...	...	x	*Perca flavescens*	
Lake Superior	...	...	x	...	*Leucichthys* sp.	
Lake Nipissing	...	...	x	...	*Esox lucius, Leucichthys* sp.	Fallis, MS, 1934
Lake Nipissing	...	...	x	...	*Esox lucius*	Ekbaum, 1937
Lake of the Woods	...	...	x	...	*Esox lucius*	
Moose Lake	...	...	x	...	*Esox lucius*	
Lake Superior	...	x	...	...	*Stizostedion vitreum*	Miller, 1945c
Lake Nipigon	...	...	x	...	*Coregonus clupeaformis*	Welch, 1951
	...	...	x	...	*Leucichthys* spp.	
Shakespeare Island Lake	...	...	x	...	*Coregonus clupeaformis*	
Manitoulin Island, South Bay	...	...	x	...	*Petromyzon marinus*	R. V. Bangham, 1952 (pers. comm.)
	...	...	x	...	*Leucichthys* sp.	
	...	...	x	...	*Coregonus clupeaformis*	
	...	...	x	...	*Esox lucius*	
Manitoulin Island, Lake Mindemoya	...	...	x	...	*Coregonus clupeaformis*	R. V. Bangham, 1952 (pers. comm.)
Muskeg Lake	...	...	x	...	*Coregonus clupeaformis*	Welch, 1950
	...	...	x	...	*Leucichthys* sp.	
	...	...	x	...	*Esox lucius*	
	...	...	...	x	*Perca flavescens*	
	...	...	...	x	*Esox lucius*	
Manitoba						
Lake Winnipeg	...	...	x	...	*Coregonus clupeaformis*	Newton, 1932
Lake Winnipegosis	...	...	x	...		
Lake Dauphin	...	...	x	...	and	
Lake St. Martin	...	...	x	...		
Lakes in The Pas District	...	...	x	...	*Leucichthys* spp.	
Lake Winnipeg	...	...	x	...	*Leucichthys*	Nicholson, 1932
Lake Kississing	...	...	x	...	*Coregonus clupeaformis*	
Lake Athapapuskow	...	...	x	...	*Coregonus clupeaformis*	
Lake Manitoba	...	...	x	...	*Leucichthys* sp.	J. J. Keleher, 1952, (pers. comm.)

TABLE I (*Continued*)

Place	Species of *Triaenophorus* spp.	*stizosted-ionis*	*crassus*	*nodulosus*	Fish species infected	Authority
Lake Winnipeg	...	...	x	...	*Esox lucius*	Ekbaum, 1937
Heming Lake	...	...	x	...	*Coregonus clupeaformis*	
	...	...	x	...	*Leucichthys* sp.	
	...	...	x	...	*Esox lucius*	
	...	...	...	x	*Lota lota lacustris*	Lawler, 1950
	...	...	...	x	*Perca flavescens*	
	...	...	...	x	*Esox lucius*	
	...	x	...	...	*Percopsis omiscomaycus*	
	...	x	...	...	*Stizostedion vitreum*	
Heming Lake	...	...	...	x	*Cottus cognatus gracilis*	Lawler, 1951
	...	x	...	...	*Cottus cognatus gracilis*	Lawler, 1953 (unpub.)
Hudson Bay drainage system						
	x	...	...	...	*Esox lucius*	
	x	...	...	...	*Coregonus* sp.	Wardle, 1932[a]
	x	...	...	...	*Leucichthys* sp.	
	x	...	...	...	*Perca flavescens*	
Nueltin Lake (partly in Manitoba)	...	...	x	...	*Coregonus clupeaformis*	Federal Dept. of Fish.
Great Bear Lake	...	...	x	...	*Cristivomer namaycush*	
	...	...	x	...	*Leucichthys* sp.	
	...	...	x	...	*Coregonus clupeaformis*	Miller, 1947
	...	...	x	...	*Thymallus signifer*	
	...	...	x	...	*Esox lucius*	
	...	...	...	x	*Thymallus signifer*	Miller, 1946
Great Slave Lake	...	...	x	...	*Cristivomer namaycush*	
	...	...	x	...	*Stenodus leucichthys*	Rawson, 1947
	...	...	x	...	*Leucichthys* sp.	
Saskatchewan						
Nesslin Lake	...	...	x	...	*Coregonus clupeaformis*	
	...	...	x	...	*Esox lucius*	
Mosher Lake	...	...	x	...	*Coregonus clupeaformis*	Wheaton and Rawson, 1949
	...	...	x	...	*Leucichthys* sp.	
	...	...	x	...	*Esox lucius*	
Lake Athabasca	...	...	x	...	*Coregonus clupeaformis*	
	...	...	x	...	*Cristivomer namaycush*	Rawson, 1947
	...	...	x	...	*Leucichthys* sp.	
	...	...	x	...	*Esox lucius*	
Alberta						
Lesser Slave Lake	...	...	x	...	*Leucichthys tullibee*	
	...	...	x	...	*Coregonus clupeaformis*	
	...	...	x	...	*Prosopium* sp.	Miller, 1943
	...	...	x	...	*Esox lucius*	
	...	...	...	x	"*Lota maculosa*"	
	...	...	...	x	*Esox lucius*	

TABLE I (*Continued*)

Place	Species of *Triaenophorus*: spp.	*stizosted-ionis*	*crassus*	*nodulosus*	Fish species infected	Authority
Lesser Slave Lake	...	...	...	x	*"Lota lota maculosa"*	Miller, 1945a
	...	...	...	x	*Esox lucius*	
Lesser Slave Lake	...	...	x	...	*Leucichthys* sp.	Miller, 1945b
	...	...	x	...	*Coregonus clupeaformis*	
	...	...	x	...	*Prosopium oregonium*	
	...	...	x	...	*Esox lucius*	
Lesser Slave Lake	...	x	...	...	*Percopsis omiscomaycus*	Miller, 1945c
	...	x	...	...	*Stizostedion vitreum*	
Northwest Territories						
Great Slave Lake	...	...	x	...	*Prosopium cylindraceum*	Rawson, 1950
	...	...	x	...	*Coregonus clupeaformis*	
	...	...	x	...	*Leucichthys* sp.	
	...	...	x	...	*Thymallus signifer*	
	...	...	x	...	*Cristivomer namaycush*	
	...	...	x	...	*Esox lucius*	
	...	...	...	x	*Esox lucius*	
	...	x	...	...	*Stizostedion vitreum*	
British Columbia and Yukon						
Teslin Lake Territory	...	...	x	...	*Esox lucius*	Clemens *et al.*, 1944
	...	...	x	...	*Coregonus clupeaformis*	
	...	...	x	...	*Leucichthys* sp.	

[a]Wardle states that *Triaenophorus* is common over the whole Hudson Bay drainage of Manitoba.

TABLE II. United States records of occurrence of genus *Triaenophorus*.

Place	Species of *Triaenophorus*: spp.	*stizosted-ionis*	*crassus*	*nodulosus*	Fish species infected	Authority
New York						
Oneida Lake	...	...	x	...	*Percopsis omiscomaycus*	Van Cleave and Mueller, 1934
	...	...	...	x	*Stizostedion vitreum*	
Lake Erie	x	...	...	...	*Percopsis omiscomaycus*	Bangham and Hunter, 1939
	...	...	...	x	*Stizostedion* sp.	
	...	...	...	x	*Catostomus commersoni*	
	...	...	...	x	*Micropterus dolomieui*	
	...	x	...	...	*Stizostedion vitreum*	R. V. Bangham, 1952 (pers. comm.)
	...	x	...	...	*Stiz. v. glaucum*	
	...	x	...	...	*Perca flavescens*	
Michigan						
inland lakes	...	...	...	x	*Notropis delicatus*	Cooper, 1918
	...	...	...	x	*Lepibema chrysops*	
	...	...	...	x	*Stizostedion canadense*	
	...	...	x	...	*Leucichthys artedi*	

TABLE II (*Continued*)

Place	Species of *Triaenophorus*: spp.	*stizosted-ionis*	*crassus*	*nodulosus*	Fish species infected	Authority
Lake Huron	...	...	x	...	*Petromyzon marinus*	L. N. Allison, 1951–52 (pers. comm.)
inland lakes	x	...	...	...	*Stizostedion v. vitreum*	
	x	...	...	...	*Leucichthys* sp.	
St. Joseph River	x	...	...	...	*Perca flavescens*	Dolley, 1933
Lake Huron	...	...	x	...	*Petromyzon marinus*	McLain, 1952
Indiana						
South Twin Lake, Lagrange Co.	...	...	x	...	*Leucichthys* sp.	W. E. Ricker, 1951 (pers. comm. — Identification made by R. V. Bangham)
Wisconsin						
Lake Pepin	...	...	...	x	"Speckled bullhead"	Pearse, 1924
	...	...	...	x	"Short-headed redhorse"	
Lake Michigan	...	...	...	x	*Catostomus commersoni*	Pearse, 1924
	...	...	...	x	*Catostomus catostomus*	
	...	...	...	x	*Micropterus dolomieui*	
	...	...	...	x	*Perca flavescens*	
Trout Lake region	...	...	...	x	*Perca flavescens*	Cross, 1938
	...	...	...	x	*Catostomus* sp.	
	...	...	...	x	*Lepomis macrochirus*	
	...	...	...	x	*Micropterus dolomieui*	
northern waters	...	...	...	x	in 12 species	Bangham, 1944
northwestern waters	...	...	...	x	in 6 species	Fischthal, 1945
Lake Michigan	...	...	x	...	*Leucichthys* sp.	H. C. Guilford, 1951 (pers. comm.)
	...	...	x	...	*Petromyzon marinus*	
Lake Superior	x	...	...	...	*Leucichthys* sp.	L. Posekany, 1951 (pers. comm.)
"various localities"	...	...	...	x	five species	E. Schneberger, 1951(pers.comm.)
Minnesota						
several lakes	...	...	x	...	*Leucichthys tullibee*	Hjortland, 1928
Lake Superior	...	...	x	...	*Coregonus clupeaformis*	Hoffman, 1941
	...	...	x	...	*Leucichthys* spp.	
Lake of the Woods	...	...	x	...	*Coregonus clupeaformis*	
	...	...	x	...	*Leucichthys* spp.	
Rainy Lake	...	...	x	...	*Coregonus clupeaformis*	
	...	...	x	...	*Leucichthys* spp.	
Lake Namakan	...	...	x	...	*Coregonus clupeaformis*	
	...	...	x	...	*Leucichthys* spp.	
Alaska						
Wood River Lakes system	...	...	x	...	*Esox lucius*	E. L. Burgner, 1954 (pers. comm.)
	...	...	x	...	*Salvelinus alpinus*	
	...	...	x	...	*Oncorhynchus nerka*	

TABLE III. Results of questionnaires sent to various workers and agencies during 1951–52.

State or Province	Authority	Species	Remarks
Quebec	G. Prevost	...	No records on hand of *Triaenophorus*.
Ontario	R. V. Bangham	*T. crassus*	Flesh cysts in sea lamprey, lake herring, whitefish and bloater from South Bay. Whitefish from Lake Mindemoya on Manitoulin Island. Mature parasites in pike, South Bay, Lake Huron, and other bays of Manitoulin Island.
Tennessee	R. V. Bangham	...	None found.
Kentucky	M. E. Clark	...	*Triaenophorus* parasites not found in Kentucky fishes.
Indiana	W. E. Ricker	*T. crassus*	Ciscoes from South Twin Lake, near the Michigan border.
Michigan	L. J. Thomas	*Triaenophorus*	Abounds in Lake Superior, Lake Michigan and numerous smaller inland lakes of northern Minnesota, Wisconsin and Michigan.
Michigan	L. N. Allison	*T. crassus*	In intestines of sea lamprey from Lake Huron.
Wisconsin	H. C. Guilford	*T. crassus*	Plerocercoids from ciscoes from Wisconsin and Michigan waters of Lake Michigan. Scolices of *T. crassus* from intestines of sea lampreys from Lake Michigan waters.
Wisconsin	L. Posekany	*Triaenophorus* sp.	Identification of *Triaenophorus* from herring of Lake Superior to species is not possible as records were destroyed in a fire.
Wisconsin	E. Schneberger	*T. nodulosus*	Found in five species of fish in various localities in the state.
Iowa	K. D. Carlander	...	No knowledge of any records as little fish parasite work done.
Missouri	P. G. Barnickol	...	No one on staff immediately concerned with parasites—no records of *Triaenophorus*.
Oklahoma	P. E. Smith	...	*Triaenophorus* not located to date.
North Dakota	O. I. Henegar	...	Little work done on parasites to date.
Wyoming	R. V. Bangham	...	None found.

In North America the known range of *Triaenophorus* lies between 42°N. latitude (Indiana, U.S.A.), northward to 67°N. latitude (Great Bear Lake, Northwest Territories, Canada) and from the lower St. Lawrence River northwesterly to Alaska. The most southerly record is for the State of Indiana and, although it has not been reported to occur in North Dakota, Illinois or Ohio, the presence of the genus in neighbouring states (see Table II) suggests that it will be found as a result of further work.

Radforth (1944), describing the distribution of Ontario fishes, found several species of fish restricted in their northern distribution in Ontario by a line extending from the western end of Lake Ontario to the southern part of Lake

TABLE IV. Species of fish from which the various species of *Triaenophorus* have been reported in North America.

	T. crassus	*T. nodulosus*	*T. stizostedionis*
Petromyzon marinus	x	...	...
Coregonus clupeaformis	x	x	...
Prosopium oregonium	x	...	...
Prosopium cylindraceum	x	...	...
Leucichthys spp.	x	x	...
Stenodus leucichthys	x	...	...
Thymallus signifer	x	x	...
Cristivomer namaycush	x	...	...
Salvelinus fontinalis	...	x	...
Salvelinus alpinus	x	...	...
Onchorhynchus nerka	x	...	...
Catostomus commersoni	...	x	...
Catostomus catostomus	...	x	...
Moxostoma rubreques	...	x	...
Notropis delicatus	...	x	...
Ameiurus sp.	...	x	...
Esox lucius	x	x	...
Esox masquinongy	...	x	...
Percopsis omiscomaycus	x	...	x
Lepibema chrysops	...	x	...
Perca flavescens	...	x	x
Stizostedion vitreum vitreum	...	x	x
Stizostedion vitreum glaucum	...	x	x
Stizostedion canadense	...	x	...
Micropterus dolomieui	...	x	...
Micropterus salmoides	...	x	...
Lepomis gibbosus	...	x	...
Lepomis macrochirus	...	x	...
Pomoxis nigro-maculatus	...	x	...
Cottus cognatus	...	x	...
Eucalia inconstans	...	x	...
Lota lota lacustris	x	x	...

Huron; however, farther west their northern limits were greatly extended. The northern limits of these fish are associated very closely with the southern limits of the genus *Triaenophorus*. Radforth concluded that time or geographical barriers were not the apparent reason for the limited occurrence of so many species in the drainage of southern Ontario and considered the problem ecological. Isothermal maps for fall, winter, spring, and the whole year appeared to have no relation, but the 70° July isotherm was very closely associated with the northern distributional limits of these fish. The accompanying map indicates the close association between the 70° July isotherm and the southern limits of distribution of the genus *Triaenophorus*. As there does not appear to be any geological or time barrier impeding the distribution of *Triaenophorus*, temperature may be the most important factor affecting distribution as the species probably requires a certain spring and early-summer minimum temperature to successfully reproduce and grow.

The key to the distribution of *T. crassus* and *T. nodulosus* would be the presence of *Esox lucius*, the definitive host, which has a very wide distribution. Darlington (1948) shows that, although present distribution of members of the genus *Esox* indicates a North American origin, neither *Esox* nor any close relative is known in the fossil record in America. There are several well preserved fossil species of *Esox* in the Oligocene and Miocene of Europe; and *Palaeoesox*, the earliest known member of the order Haplomi, to which the pike belongs, is found in the Eocene of Europe (Berg, 1936). Thus the pike in Europe is more likely a survivor of a receding group rather than an immigrant from America. The pike is one of the few true freshwater fishes in the Arctic and its tolerance for cold probably enabled it to cross a late Siberian-Alaskan land bridge and enter America. In British Columbia the pike is found only in the extreme northern part, which indicates entry from the lower Yukon River basin and lends authority to the hypothesis that entry to North America was by way of a Siberian-Alaskan land bridge. If the pike entered North America via a Siberian-Alaskan land bridge then it seems likely that the genus *Triaenophorus* also had its origin in Eurasian stock, as *T. crassus* and *T. nodulosus* appear together in some lakes and not in others and occur in many of the same intermediate hosts, but have been found as adults only in the pike. The abundance of *Triaenophorus crassus* in *Oncorhynchus nerka* and *Esox lucius* in the lakes of the Bristol Bay region of Alaska further substantiates the supposition that *Triaenophorus* entered North America from Asia, especially as these species of fish occur on both sides of the Pacific Ocean. *T. stizostedionis*, having the yellow walleye, *Stizostedion v. vitreum*, as its final host, has not been found in Europe or Asia. This may cast some doubt on the movement of the genus from the Old World to North America. However, it is quite possible that the species has become extinct there, as Darlington suggests the principle that centres of evolution and dispersal are likely to be also centres of extinction.

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Experimental Infection of Atlantic Cod with a Larval Marine Nematode from Smelt[1,2]

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ABSTRACT

Atlantic cod (*Gadus callarias*) and at least 13 other species of fish in Canadian Atlantic waters are intermediate hosts for a larval nematode (*Porrocaecum decipiens*). It is pointed out that large cod feed occasionally on infected species of fish and that, as a result, they may become infected. Experiments showed that when larval *Porrocaecum* from smelt (*Osmerus mordax*) were fed to cod, some worms passed through the wall of the stomach, crossed the coelom, and penetrated the hypaxonic muscle of the cod. It was concluded that *Porrocaecum* larvae, under natural conditions, are also able to pass from one species of fish to another.

INTRODUCTION

Larval ascarids of the genus *Porrocaecum* Railliet and Henry 1915 occur commonly in the musculature and viscera of the Atlantic cod, *Gadus callarias* Linnaeus 1758, in Canadian Atlantic waters (Scott, 1950). The writer (1953) has identified some of the nematodes as *P. decipiens* (Krabbe) 1878, a species whose definitive hosts are frequently seals, such as the harbour seal, *Phoca vitulina* Linnaeus 1758. The larvae are not confined solely to the Atlantic cod, but have also been observed by the author in a wide variety of marine fishes:

Smelt–*Osmerus mordax* (Mitchill)
Redfish–*Sebastes marinus* (Linnaeus)
Mailed sculpin–*Triglops ommatistius* Gilbert
Shorthorn sculpin–*Myoxocephalus scorpius* Linnaeus
Longhorn sculpin–*M. octodecemspinosus* (Mitchill)
Sea raven–*Hemitripterus americanus* (Gmelin)
Eelpout–*Macrozoarces americanus* (Bloch and Schneider)
Greenland cod–*Gadus ogac* Richardson
Hake–*Urophycis tenuis* (Mitchill)
Plaice–*Hippoglossoides platessoides* (Fabricius)
Yellowtail flounder–*Limanda ferruginea* (Storer)
Winter flounder–*Pseudopleuronectes americanus* (Walbaum)
Witch flounder–*Glyptocephalus cynoglossus* (Linnaeus)

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Many of these species, as well as small cod, may form part of the diet of large Atlantic cod. In the Bras d'Or Lake, Nova Scotia, the author observed that large cod occasionally fed on smelt, winter flounder and smaller cod. An idea of the size of the prey is indicated by the following observations: (1) five smelt, 15 to 20 cm. in length, were found in the stomach of a cod, 57 cm. in length; (2) two cod, 32 and 35 cm. long, were recovered from the stomach of an 84-cm. cod. Each cod stomach also contained *Porrocaecum* larvae: the former, a single worm, and the latter, 10 worms ranging in length from 35 to 44 mm. Worms were also noted in the muscles of the ingested smelt and cod. The occurrence of *Porrocaecum* larvae in the stomachs of these two cod was most interesting because they do not habitually occur in this location (*Porrocaecum* larvae were observed in four of 81 stomachs from infected cod), and their association with infected food fishes suggested that large cod might normally acquire many of their worms by eating smaller infected fish.

In other words, *Porrocaecum* larvae may be capable of leaving the tissues of an ingested fish, of penetrating the walls of the alimentary tract of the predator, and of finally establishing themselves in the tissues of a new host. This ability would be extremely valuable to the parasite since it would permit its survival, in spite of the loss of the original fish host, through transference from one intermediate host to another until such time as the host was eaten by a seal. If this interpretation is correct, the life cycle of the parasite may involve a succession of fishes, perhaps of various species, as intermediate hosts.

The potential complexity of this phase of the ascarid's life-history justified an attempt to verify this speculation. Since the speculation could not be supported conclusively by field observations alone, experiments were carried out in 1949 to test the specific hypothesis that *Porrocaecum* larvae from smelt, if introduced into the stomach of an Atlantic cod, were capable of establishing themselves in the muscle tissues of the cod.

METHODS

The cod used were caught near Letete Passage, Passamaquoddy Bay, New Brunswick, and were kept alive in tanks of running sea-water at the Atlantic Biological Station. The fish were fed exclusively on herring (*Clupea harengus* Linnaeus 1758) throughout the experiments, with the exception of one cod (test animal 1) which was fed live smelt. Herring were used because *Porrocaecum* larvae apparently do not occur in this fish in the region around St. Andrews.

Two experimental methods were used. In the first, a cod was permitted to feed only on live smelt which had been taken from a sample of smelt with a known incidence of worm infection. Although this method had the advantage of following as closely as possible the supposed natural sequence of events, it lacked preciseness in that it was impossible to know exactly the number of worms present in the smelt eaten by the cod. Accordingly a more accurate method was adopted: *Porrocaecum* larvae were removed from the muscles of smelt and inserted, usually immediately, in known quantities into the mouths of recently killed herring which were then fed to a cod. Although it was desirable

to use small cod because of the lower incidence of natural *Porrocaecum* infection in small cod, this was not always practicable as the most active feeders were usually the larger individuals. Consequently the latter were used, if necessary, to ensure that the herring containing the worms were swallowed at once by the test animal before the worms could escape from the herring. At various times following the introduction of the worms, test animals were killed. The alimentary tract of each test animal was opened and all nematodes contained therein were preserved. In test animals 4, 5 and 6 only, the alimentary mucosa was examined carefully for marks or areas of inflammation. Finally, the number as well as the position and condition of the worms in the musculature and body cavity were carefully noted.

The position and condition of worms in cod yields, in a general way, some information about the length of time worms have been in the fish; recent arrivals can be distinguished from larvae of long residence in the host. Inasmuch as information of this type is pertinent to the present account, a brief description of the appearance and distribution of the larvae in cod is essential as a background for the interpretation of the experimental results. The following description is based upon observations made on about 3,000 cod.

Although the worms often lie free and uncoiled within the muscle, more frequently they are tightly coiled and enclosed in a capsule or sheath of connective tissue, presumably derived from host tissues. Several stages in the development of the capsule can be recognized, passing from an initial stage in which a worm lies completely free in the muscle to the final stage of a rough, brown capsule containing the necrotic remains of a worm. The fact most relevant to this account is that the process of encapsulation is slow and probably extends over a period of several years; it was observed that encysted worms did not occur in yearling cod and that the frequency of cysts, particularly those of the later stages, increased in older fish. Therefore, a worm, if even partially encysted, should not be considered to be a recent arrival in the tissues of the host.

A second relevant observation was that larval *Porrocaecum* were very rarely seen in an unencysted state in the coeloms of cod, and only twice were worms seen penetrating the peritoneum. Thus the probability of observing this phenomenon under natural conditions is obviously slight. Accordingly, if, in the experiments, worms were found crossing the coelom or penetrating the peritoneum, then such observations would suggest that the worms so observed were part of those artificially introduced.

The amount of infection in the test cod before the experiments was unknown. However, the amount of infection was accurately determined for 32 cod caught at the same time as the experimental fish and it has been assumed that the latter group of fish before the experiments would have had a similar incidence of infection. The method of control for the experiments was admittedly not entirely satisfactory. When the majority of the control animals were killed, the author did not fully appreciate the significance of variations in the degree of encystment of the worms within the host and no notes were made on the encystment of worms in the control fish. With that exception, however, similar informa-

tion was recorded for worms from both the control and the experimental groups of fish.

OBSERVATIONS

Table I shows the numbers of *Porrocaecum* larvae found in the control animals.

TABLE I. Numbers of *Porrocaecum* larvae observed in 32 cod caught near Letete Passage, N.B., on May 19, 1949. Total lengths of cod are in centimetres. Twenty-eight specimens were killed on May 19. Of the remainder (marked by asterisks), the first three were killed on July 21 and the fourth on September 8.

Length of cod	Number of worms	Length of cod	Number of worms
cm.		*cm.*	
41	2	54	1
43	0	56	1
43	2	*56	7
43	3	57	0
44	0	58	6
44	0	60	5
45	2	61	1
46	1	61	2
46	1	*62	0
48	1	62	1
49	1	63	4
49	1	*64	0
51	1	*65	1
52	2	67	25
53	2	68	1
53	2	71	0

The amount of infection in the controls was low; the mean number of worms per fish was 2.56. Fewer than five worms were seen in each of 28 fish (87.5 per cent of the sample) and only one fish of the remainder had more than seven worms. In 18 fish, 31 worms were found in the epaxon and eight in the hypaxon. No worms were observed in the coeloms or digestive tracts of the control fish.

No marks of inflammation were noted in the mucosa of the alimentary canal of four control cod examined specifically for this characteristic.

Table II contains the results of the feeding experiments and the essential features of the results are summarized below.

Each of the six fish in the experimental group contained more than seven worms; the mean number of worms per fish for this group was 10.50 (9.67 if the five moribund worms in test animal 5 are excluded). Twenty worms were recovered from the epaxonic muscle and 21 form the hypaxonic. Each fish contained worms either in the stomach or in the coelom; a total of 22 worms were

present in these locations. Three worms were observed penetrating the peritoneum. No worms were found in the intestine.

Marks of inflammation on the gastric mucosa or submucosa were noted in the three fish examined for areas of inflammation.

TABLE II. Results of 1949 experiments on the introduction of *Porrocaecum* larvae from smelt into 6 cod. The cod were held in a tank and fed either whole smelt or worms removed from them. After 18 hours to 6 days, the cod were killed and examined for worms in the stomach, intestine, coelom and muscles.

Cod No. 1. 63 cm. Ten smelt were placed in the tank on May 27, and on June 2 all had been eaten. Autopsy on the latter date showed 3 *Porrocaecum* in the coelom and 4 in the epaxial muscles—7 in all. The smelt used were taken from a sample with worm incidence of 35 per cent; in the original sample, the mean number of worms per fish was 0.67. No observations were made on inflammation in digestive tract. The worms in the coelom were free and active; one had penetrated the peritoneum and sub-peritoneal muscle to an extent of 15 mm. All worms in epaxial muscle were encysted.

Cod No. 2. 41 cm. Fed 15 worms from smelt on July 4. Autopsy after 48 hours showed 1 *Porrocaecum* in the coelom, 7 in the hypaxial muscles, and 1 in the epaxial muscles—9 in all. No observations were made on inflammation in digestive tract. The worm in the coelom was free and active. One of the 7 worms found in the hypaxial muscle was encysted; of the remainder, 3 were surrounded by inflamed tissue. The worm in the epaxial muscle was not encysted.

Cod No. 3. 70 cm. Fed 10 worms from smelt on July 4. Autopsy after 48 hours showed 1 *Porrocaecum* in the coelom, 7 in the hypaxial muscle and 7 in the epaxial muscle—15 in all. No observations were made on inflammation in digestive tract. A worm was coiled, but not encysted, on dorsal mesentery. No worms in hypaxial muscle were coiled or encysted. Three worms were close together near the lateral septum, lateral to distal ends of ribs, about 1 cm. through muscle from coelom; there was extensive inflammation of the sub-peritoneal connective tissue in this region. Four worms in epaxial muscle were encysted.

Cod No. 4. 52 cm. Fed 10 worms from smelt on July 6. Autopsy after 22.5 hours showed 2 *Porrocaecum* in the stomach, 4 in the coelom, 5 in the hypaxial muscle and 4 in the epaxial muscle—15 in all. The stomach contained 2 active larvae. Five spots of inflammation, each about 1 mm. in diameter, were observed in the mucosa. Extensive inflammation was present in the submucosa. No inflammation was seen in the intestine. Four worms were in the coelom: two were free and active, one had entered the liver in the vicinity of the bile duct to an extent of about 3 mm., and the fourth had penetrated about 4 mm. into the peritoneum and underlying muscle at the posterior end of the coelom. No encystment was seen in the worms in the hypaxial muscle. One worm in the epaxial muscle was encysted.

Cod No. 5. 42 cm. Fed 10 worms from smelt on July 19, 5 of which had been removed from smelt a week previously. Autopsy after 18 hours showed 7 *Porrocaecum* in the stomach and 3 in the coelom—10 in all. The stomach contained 7 worms of which 5 were apparently moribund; the other 2 were active. The coelom contained 2 free and active worms near the pyloric caeca and a third which had penetrated about 2 mm. into the peritoneum opposite the duodenum. Two spots of inflammation were observed on the mucosa of the stomach.

Cod No. 6. 56 cm. Fed about 6 worms from smelt on July 20. Autopsy after 24.5 hours showed 1 *Porrocaecum* in the stomach, 2 in the hypaxial muscle and 4 in the epaxial muscle—7 in all. The stomach contained an active larva. Three marks of inflammation, each about 1 mm. in diameter, were observed on the mucosa; extensive inflammation was noted in the muscularis mucosa. Hypaxial muscle contained 2 worms which were neither coiled nor encysted and which were surrounded by inflamed tissue. All worms in epaxial muscle were heavily encysted.

DISCUSSION

There was a great difference in the amount of infection present in the two groups of cod. The means and variances of the two samples were tested statistically by means of the "t" test and a test of the homogeneity of variance (Snedecor, 1946, pp. 80 and 249). The former test yielded a P value < 0.01 and the latter a P value > 0.10. On these bases it is concluded that the mean number of worms in the two samples were significantly different. The possibility that the amount of infection might increase naturally in larger fish was also considered and the mean lengths of the two samples were also tested statistically in a similar fashion. In the "t" test a value of $P > 0.90$ was obtained, a value which indicates very strongly that the two samples were not different with respect to their lengths. It is therefore concluded that the larger infection in the experimental group resulted from the artificial introduction of worms.

Not only was there a difference in the amount of infection in the two groups, but there were also notable differences in the distribution of the worms in the two groups of fish. In the control group, a large majority of the worms were present in the epaxon; in the experimental animals, the worms were almost equally divided between the epaxon and the hypaxon. If the spatial relationships of these areas to the coelom are considered, it will be obvious that most worms upon leaving the coelom must first enter the hypaxon before the epaxon can be reached. Thus worms in the hypaxon will generally have been of more recent arrival in the host than those in the epaxon. Continuing this argument, the much higher number of worms in the hypaxon of the experimental fish suggests at once that at least some of these worms had only recently entered the hypaxon. Additionally indicative of a recent arrival was the fact that many worms in the experimental fish were lying uncoiled close to the peritoneum amid areas of inflamed muscle. It is also significant that in the experimental fish no worms in the hypaxon were encysted, whereas 13 out of 20 worms in the epaxon showed some signs of encystment. In view of what was said earlier about the rate of encystment it is clear that most of the worms in the epaxon had been longer in the host than those in the hypaxon. These observations support the conclusion made earlier that the higher incidence in the experimentals was primarily the result of the feeding experiments.

Even stronger evidence is available when it is emphasized that 22 worms were recovered from the coeloms or stomachs of the experimental group. It was remarked earlier that such observations on normal cod were very rare; the probability of worms occurring by chance alone in either of those regions in each of the six test animals is thus very slight and the worms in the coelom are likely some of those introduced earlier.

The passage of some worms from the stomach to the coelom is also confirmed by the presence of areas of inflammation on the mucosa and submucosa of the stomachs of some experimental fish. Such marks were not observed in the stomachs of four control animals; therefore, the marks in the experimental animals were probably caused by the movement of worms through the wall of the stomach.

To sum up, there is strong evidence to show that at least some of the worms from smelt introduced into the test cod succeeded in passing through the wall of the stomach, into the coelom, and thence into the axial musculature. There is no evidence that the passage from the digestive tract to the body cavity took place through the walls of the intestine.

The time required for the worms to pass from the stomach to the body wall was in most cases less than 48 hours. Test animal 3, killed after 48 hours, contained no worms in the digestive tract or coelom; test animal 2, also killed after 48 hours, contained one worm in the coelom. Test animals 4 and 5, killed after 22.5 hours and 18 hours, respectively, each had worms penetrating the peritoneum; at the same time each fish still had some worms in the stomach. Thus, apparently more than 24 and less than 48 hours were needed for the majority of the worms to complete their movement into the body wall.

These experiments were undertaken to determine if *Porrocaecum* larvae from smelt were capable of infecting a new intermediate host, in this case, cod. Such an ability was demonstrated by the experiments. However, the results of the experiments admittedly do not conclusively prove that this process proceeds under natural conditions, although, in this connection, the results from test animal 1 tend to support the view that the transfer of worms from one species of fish to another may occur naturally. Moreover, the experiments do not show either that the worms introduced into the tissues of the new host were completely viable or that they would have remained alive for a normal period of time. Nevertheless, the experimental evidence, in conjunction with the field observations cited earlier, indicates strongly that cod under natural conditions may become infected by eating infected smelt.

The wide variety of fishes in which *Porrocaecum* larvae may dwell implies a wide range of physiological tolerance by the larvae; that is, there is no indication that the parasite is restricted to any particular species, genus, or even family of fish. This being so, it is likely that cod can become infected, not only by eating infected smelt, but also by eating other species of fish which harbour the parasite. Thus, this stage of the ascarid's life-cycle may be extremely complex, involving a succession of fishes acting as facultative intermediate hosts.

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Osmophilism of *Sporendonema epizoum*[1,2]

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ABSTRACT

Shake-culture studies of the fungus *Sporendonema epizoum*, commonly called "dun", indicated that glucose, sodium nitrate and potassium chloride could replace the sodium chloride generally considered necessary to initiate growth. It was therefore concluded that this organism is an obligate osmophile rather than an obligate halophile.

There have been several suggestions in the past that microorganisms which are obligate halophiles might in reality be obligate osmophiles. Work of particular interest in this regard is that of Flannery *et al.* [1]. These workers demonstrated that the sodium chloride considered necessary for the growth of *Vibrio costicolus* could be replaced by other electrolytes. However, in a later paper [2] they were of the opinion that an osmotic pressure explanation of halophilism would not suffice because the organism would not grow in non-electrolytes.

This paper presents data on the effect of various concentrations of electrolytes and a non-electrolyte on the growth of *S. epizoum* (Corda) Ciferri et Redaelli. This fungus is better known to the fishing industry as "dun", so-called because its brown spores discolour salt fish.

METHODS

CULTURE. The culture was isolated from salt fish and was maintained on slants of the basal medium containing 12 per cent sodium chloride and 1.5 per cent agar.

MEDIUM. A satisfactory basal medium was prepared by adding 10 g. glucose, 10 g. casein hydrolysate, 1 g. sodium chloride, 1 g. dipotassium phosphate, 0.2 g. magnesium sulphate, 0.02 g. ferrous sulphate to 1 litre of distilled water. Solutions ranging from O to 5 M in either sodium chloride, sodium nitrate, potassium chloride, or glucose were made up in the basal medium and dispensed in 23-ml. amounts into 125-ml. Erlenmeyer flasks. These media were sterilized by heating at 100°C. for ½ hour on three successive days. The pH of the solutions was unadjusted but fell between 6.5 to 7.0 depending on the concentration of the salts or glucose.

INOCULATION AND INCUBATION. The surface growth from a slant culture in a 2-oz. bottle was transferred to 100 ml. of 10 per cent salt solution and filtered through No. 1 Whatman filter paper to remove pieces of agar and clumped cells. Two ml. of the resulting spore suspension were inoculated into each flask of medium and these cultures were incubated on a reciprocating culture shaker at

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25°C. Since it was not possible to have more than 50 flasks on the shaker at one time, the results are reported from three separate experiments.

HARVESTING CELLS. After shaking the cultures for 14 days, the growth in the flasks was harvested by filtering with suction through No. 2 Whatman filter paper in a Gooch crucible. The cells were washed with 25 ml. of 5 or 10 per cent salt solution, depending on the concentration of the medium surrounding the cells. This washing procedure did not cause a significant loss of protein through plasmoptysis. This point was tested by suspending about 50 mg. of cells grown in 2.5 M sodium chloride solution in 2 ml. of distilled water. After 10 minutes, the cells were centrifuged out and the supernatant tested for protein with a biuret reagent. Since no protein could be detected, and since the protein content of mould mycelium reportedly [3] ranges from 13.7 to 43.7 per cent, it was concluded that any losses through plasmoptysis were within the experimental error. After washing, the mycelium was transferred to a tared 10-ml. beaker, dried overnight at 85° to 90°C., and weighed to determine the dry weight of the cells.

RESULTS AND DISCUSSION

From the results presented in Figure 1, it is evident that glucose served as well as sodium chloride as a growth-permitting factor for *S. epizoum*. Table I shows that other salts can also replace sodium chloride. Since growth of *S. epizoum*, formerly thought to be an obligate halophile [4], was stimulated by each of these different compounds in turn, it would appear that none satisfied a nutritional need of the organism. This being so, their mutual effect must be to condition the physical environment to permit growth.

Stuart [6] suggested that there might be a correlation between the growth of red halophilic bacteria in sodium chloride and the reduction of the oxygen tension of the medium caused by the decreasing solubility of oxygen with increasing concentrations of the salt. However, this explanation does not suffice for *S. epizoum* because it is a strict aerobe as determined by the method of Spray [5], and by incubating newly inoculated cultures in an atmosphere in which 13 per cent of the air was replaced by carbon dioxide.

A more likely explanation of the mutual function of the salts and glucose is that they produce a favourable osmotic pressure for the growth of *S. epizoum*. This hypothesis is strengthened when it is recalled that osmotic pressure is mainly dependent on the number of particles in solution. Thus a mole of a salt

TABLE I. Growth response of *S. epizoum* to various concentrations of salts, measured as dry weight in mg. Figures shown are averages of duplicate flasks.

	Molarity				
	0	1	1.5	2	2.5
NaCl (control)	0	32 ± 0	75 ± 2	84 ± 8	100 ± 6
KCl	0	35 ± 4	68 ± 0	73 ± 0	76 ± 4
$NaNO_3$	0	60 ± 8	65 ± 0	61 ± 4	70 ± 1

such as sodium chloride, which dissociates into 2 ions, would be expected to have twice the osmotic pressure of a mole of glucose. Figure 1 shows that it takes 0.5 M sodium chloride or 1 M glucose to initiate growth. There were not enough replicates to establish the shape of the curves either for glucose or for sodium chloride with accuracy. However, there is nothing in the data to suggest that the upward slope of the curves negates the osmotic pressure hypothesis.

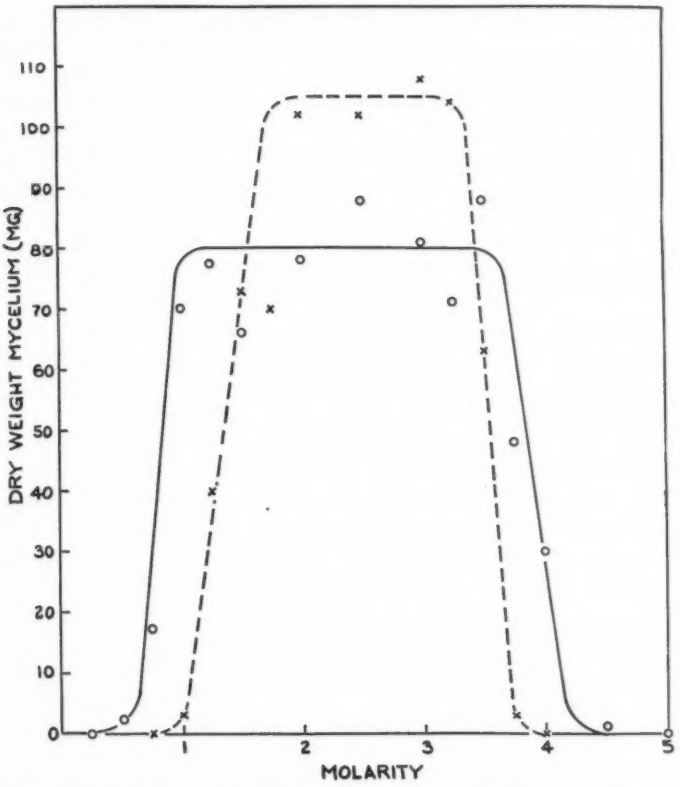

FIGURE 1. Growth response of S. *epizoum* to various concentrations of glucose (dotted line) and sodium chloride (solid line). Data averaged from triplicate flasks.

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Taxonomic Characters of the Eastern North America Chars (*Salvelinus* and *Cristivomer*)[1,2]

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ABSTRACT

For the present study about 300 specimens have been examined. These specimens belong to the six species of chars: *C. namaycush*, *S. fontinalis*, *S. aureolus*, *S. oquassa*, *S. marstoni*, and *S. alpinus*. Among meristic characters, the number of pyloric caeca was found to be very important. Body proportions and meristic characters, such as fin rays and vertebrae, are inadequate to properly describe a species. On the other hand, the skull bones, different teeth, and skeleton of the tail are sufficient in themselves to define a species. The pearl organs were found only in *C. namaycush* of both sexes. The taxonomic relation between species is as follows: *C. namaycush* belongs to a distinct genus; *S. fontinalis* represents a subgenus *Baione*; while the remaining chars are grouped in a subgenus *Salvelinus*.

CONTENTS

Introduction	904
List of Species	905
Taxonomic Characters	905
Embryonic stages	905
Body proportions	906
Meristic characters	909
Skeleton	913
Coloration	913
Sexual dimorphism	923
Weight	925
Habitat	927
Number of chromosomes	927
Hybrids	927
Conclusions	928
Acknowledgments	929
Résumé	930
References	930

INTRODUCTION

Apparently no paper dealing with critical reviews of taxonomic characters in chars as a group, has ever been published. Even such well-known works as that by Jordan and Evermann (1896, pp. 483–516) or Kendall (1914) do not contain sufficient information. The aim of the present paper is to close up to some extent the lacunae in our knowledge.

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LIST OF SPECIES

From Eastern North America several chars have been described, at least six of which have been generally recognized as distinct species. Brief chronological data of these discoveries are as follows:

1. *Cristivomer namaycush.* In 1792, Walbaum described this new species, the lake trout, from the Hudson Bay area, based on the *Namaycush salmon* of Pennant (1792, p. 191). Certain authors (Regan, 1914; Kendall, 1914; Walters, 1953; etc.) include *C. namaycush* in the genus *Salvelinus*, while the others (Kendall, 1919; Stokell, 1951; Vladykov and Corson, 1953; etc.) consider *Cristivomer* as a distinct genus. Regardless of the exact taxonomic position of the lake trout, it has many features in common with the chars, hence it is included in the present paper.

2. *Salvelinus fontinalis.* In 1815 Mitchill brought to light existence of this species from a locality near New York city. It is variously called speckled trout, speckled char, brook trout or Eastern brook trout. *S. agassizi*, discovered by Garman in 1885 from Dublin Pond, New Hampshire, and *S. timagamiensis* described in 1925 by Henn and Rinkenbach from Timigami region, Ontario, are merely colour varieties of the common speckled trout.

3. Group of *Salvelinus alpinus.* Richardson from 1823 to 1836 described from the Canadian Arctic 5 species of arctic chars, placed by him in the genus *Salmo*: *alipes, hearnei, hoodi, nitidus,* and *rossi.* Some of these are probably closely related or even identical to certain of four species of chars (*alpinus, carpio, rivalis,* and *stagnalis*), reported from Greenland by Fabricius in 1780. Günther in 1878 added two more species (*naresi* and *arcturus*) from Cumberland Gulf and Victoria Lake in the Canadian Arctic. Moreover, Berg (1948, pp. 269–295) recognized 11 species of chars from the Russian Arctic alone. As the taxonomy of arctic chars has not been worked out sufficiently, in using the name *S. alpinus* throughout the present paper, we refer, not to a single species, but to a group of different forms.

4. *Salvelinus oquassa.* In 1854 Girard described the "blueback trout" from Moosemegantic Lake, one of the Rangeley lakes, Maine.

5. *Salvelinus aureolus.* In 1877 Bean established this new species, known as either "golden" or "Sunapee" trout, found in certain lakes of New Hampshire and Maine.

6. *Salvelinus marstoni.* In 1893 Garman described this species, generally known today as "red Quebec" trout, from Lac de Marbre, Ottawa County, Quebec.

TAXONOMIC CHARACTERS

Published data and personal experience have taught us that for proper identification of Salmonidae, the following suggestions should be applied.

Embryonic Stages

Although in taxonomic papers references to stages previous to hatching are usually lacking, there is no reason to exclude them. In effect, a developing egg of speckled trout has the same right as an adult to be considered as *S. fontinalis.*

We have found sufficient specific differences in the case of *eyed eggs* and *sac fry*. These differences consist of the diameter of the egg or size of fry and degree of their pigmentation (Table I). The smallest size and the darkest pigmentation is typical of S. *fontinalis*. Large size and weak pigmentation separate *C. namaycush*. Fry of *Salmo salar* are particularly large and practically without pigmentation. Unfortunately we have been unable to obtain, as yet, material on *Salvelinus marstoni, S. oquassa* and *S. alpinus*. The diameter of eggs of the arctic char is quite large, comparable to that of eggs of the lake trout (Vladykov, 1933, p. 20; Grainger, 1953, p. 359). Additional details, together with illustrations, will be published in a separate paper.

TABLE I. Embryonic stages of different Salmonidae. Average data for 10 specimens.

Species	Origin	Eyed egg		Sac fry		Pigmentation of embryo[a]
		Diameter	Weight	Total length	Weight	
		mm.	*g.*	*mm.*	*g.*	
S. fontinalis	New Hampton, N.H.	4.0	0.040	13.9	0.040	+++
	L. Jacques-Cartier, P.Q.	4.4	0.040	15.0	0.033	+++
S. aureolus	New Hampton, N.H.	4.7	0.050	17.1	0.055	++
C. namaycush	Twin Mountain, N.H.	5.7	0.125	19.1	0.075	+
	Baldwin's Mills, P.Q.	5.8	0.125	16.2	0.080	+
S. salar	Pollitt Riv., N.B.	5.4	0.090	16.0	0.110	(+)
	Gaspé, P.Q.	6.8	0.200	17.4	0.180	(+)

[a]The higher number of crosses corresponds to the greater development of pigmentation. (+) indicates an extremely weak degree of pigmentation.

Body Proportions

In order to make a comparison between specimens older than sac fry, they should be treated according to their stages of development. These stages are as follows:

(i) parr
(ii) adolescents (smolts) of both sexes
(iii) spawning females
(iv) spawning males.

On each specimen, 40 different measurements were made. Of this number only 16 were found to be particularly useful (Fig. 1) and henceforth will be discussed in the present paper. These measurements are as follows:

1. Total length (T.L.).
2. Fork length (F.L.).
3. Head length (H.L.).
4. Maxillary length (mx.).[3]
5. Snout length (m.).
6. Post-orbital head length (p.o.).
7. Interorbital width (i).
8. Distance between the snout and the insertion of the ventral (m-V.).

[3]Wilder (1952, p. 177) in his length of the "upper jaw" included both the premaxillary and maxillary, while in our case only the maxillary is used.

9. Distance between the snout and the insertion of the dorsal (m-D.).
10. Distance between insertions of the pectoral and ventral fins (p-V.).
11. Distance between insertion of the ventral and anal fins (V-A.).
12. Length of pectoral fin (P.).
13. Length of ventral fin (V.).
14. Length of the caudal peduncle (c.p.).[4]
15. Greatest body depth (H.).
16. Depth of tail fork, i.e. the difference between total and fork lengths (f.).

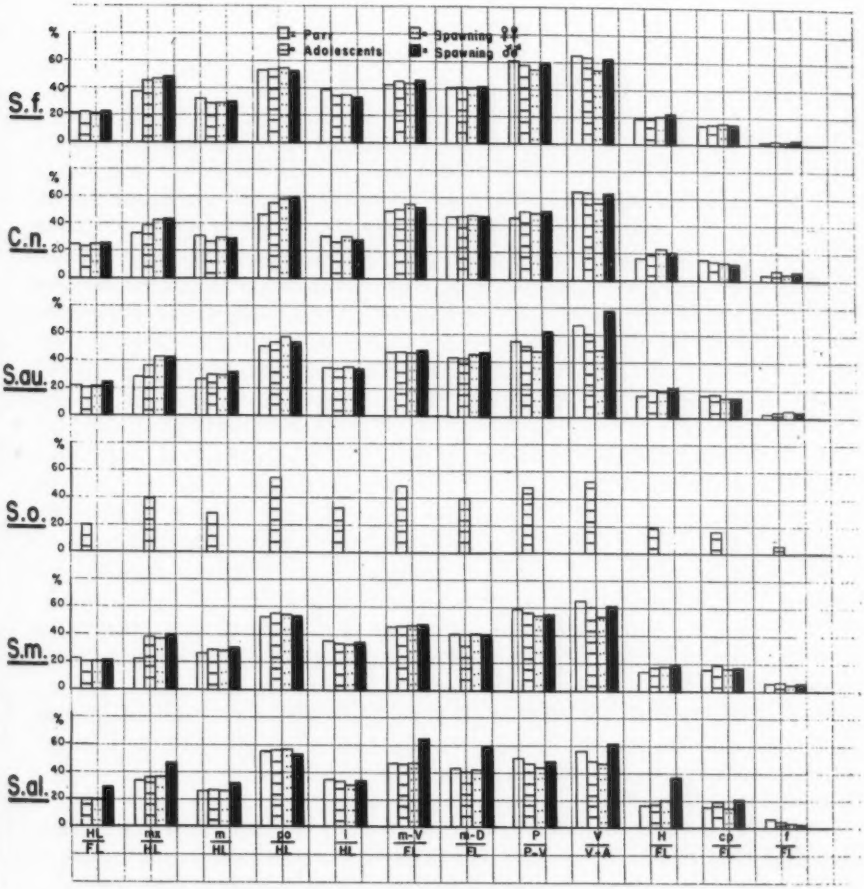

FIGURE 1. Variations, according to stages, in the body proportions in different chars, expressed in percentages of either the fork length (F.L.) or head length (H.L.). Data are in averages. For number of specimens in each stage see Table II and for explanation of other designations see text.

[4]The caudal peduncle was measured to the vertical groove at the base of the caudal fin.

Table II contains information on the number of specimens in each stage. As the purpose of these data was to show a general trend in the variation of different characters, a small number of specimens was sufficient.

TABLE II. Number of specimens, according to stages, studied for body proportions.

Species	Number of specimens in each stage				
	Parr	Adolescents	Spawning ♀♀	Spawning ♂♂	Total
S. fontinalis	10	17	12	10	49
C. namaycush	10	28	5	10	53
S. aureolus	20	22	1	1	44
S. oquassa	...	5	...	...	5
S. marstoni	4	32	25	20	81
S. alpinus	11	10	2	1	24
Total	55	114	45	42	256

The principal differences between young and adult specimens are the diameter of the eye and the length of maxillary. From Figure 1 it is quite apparent that in a number of characters the spawning males are different from females and young of their own kind. In the following discussion on body proportions spawning males will be excluded, as their peculiarities have direct bearing on the sexual dimorphism, which will be described later in this paper.

(*a*) *Head length.* This measurement, expressed in percentage of the fork length, is the greatest in *C. namaycush,* around 24, while in the remaining species it is less than 22.

(*b*) *Maxillary length.* In parr of all chars, this bone is much shorter than in adult stages. Among different species, S. *fontinalis* has the longest maxillary, the length of which, expressed in percentage of head length, varies from 46 to 48.

(*c*) *Interorbital width.* This measurement, expressed in percentage of the head length, is smallest (27–31) in *C. namaycush* and is largest (34–39) in S. *fontinalis.* In the remaining species it varies from 32 to 36.

(*d*) *Distance between snout and the base of the ventral fin.* In the case of *C. namaycush,* this distance, expressed in percentage of the fork length, varies from 50 to 55, while in the remaining species it is from 43 to 49.

(*e*) *Distance from the snout to the front of the dorsal.* It is again *C. namaycush* which has the greatest distance, varying from 46 to 48% of the fork length. In the remaining species the dorsal fin is placed closer to the head, with a distance from 40 to 46%.

(*f*) *Greatest body depth.* In the case of parr, the body of which is more elongated than that of adults, this measurement is very characteristic. Young of S. *fontinalis* have a depth of 19.4% of the fork length, whereas in the remaining species this measurement varies from 14 to 16% only.

(*g*) *Depth of the tail fork.* Among our chars, only S. *fontinalis* has a caudal fin which is little forked, the depth of which is typically less than 3% of the fork length. The tail of the other species is rather strongly forked, being usually from 4 to 7%.

Although the taking of measurements and making of calculations require considerable time, their taxonomic value is rather smaller than would be expected. For variations in body proportions of the fish, which are the same genetically but exposed to different water temperatures, see Martin (1949).

MERISTIC CHARACTERS

In this category we include the following:

(*a*) Number of scales.
(*b*) Number of branchiostegal rays.
(*c*) Number of gill-rakers.
(*d*) Number of vertebrae.
(*e*) Number of fin rays.
(*f*) Number of pyloric caeca.

(*a*) *Scales.* All species of chars have rather small scales and their number is nearly the same, about 200 lateral rows; thus this character was not considered by the present author to be at all useful. Moreover, as Mottley (1934) showed for the Kamloops trout and Wilder (1952, p. 188) for speckled trout, the number of scales could be easily influenced by different temperatures.

(*b*) *Branchiostegals.* The number of branchiostegal rays has a certain taxonomic value. The highest number (12.9 on the average) was found in *C. namaycush.* In the remaining chars, it is about the same, being on the average from 10 to 11. Moreover, the number of branchiostegals on the right side of the fish in all chars is somewhat smaller than on the left. It should be added that there is no variation in the number of branchiostegals with the age of the fish (Table III). According to Wilder (1952, p. 186), in a lot of speckled trout fry hatched at a very low temperature the number of branchiostegals was somewhat smaller, namely 10.26, than in another lot from the same parents hatched at a higher temperature (10.76 rays).

(*c*) *Gill-rakers.* This character, which is a favourite with those who study Coregonidae, is apparently of very little value for chars. First of all, the number of gill-rakers varies with age (Table V), and in dissecting gill arches very often some rakers may be cut off. Moreover, at both ends of the gill arch rudimentary rakers are often present, which apparently are included in the total counts by

TABLE III. Number of branchiostegal rays on the left side. Based on the number of specimens (N) indicated.

Species	N	Branchiostegal rays							
								Average	
		9	10	11	12	13	14	Left side	Right side
S. fontinalis	59	1	19	27	12	...	...	10.8	10.3
C. namaycush	36	...	...	...	6	28	2	12.9	12.4
S. aureolus	34	2	13	17	2	...	...	10.6	10.2
S. oquassa	4	...	4	...	...	...	...	10.0	10.0
S. marstoni	43	4	34	5	...	...	...	10.0	9.7
S. alpinus	12	...	3	6	3	...	...	11.0	10.1

certain authors, and excluded by others. In general, speckled trout has the smallest number (17.7 on the average) and arctic char has the highest (21.3). Our data suggest also that the number of gill-rakers on the right side is somewhat higher than that on the left (Table IV).

TABLE IV. Number of gill-rakers on the left side.

Species	N	Gill-rakers													Average	
		15	16	17	18	19	20	21	22	23	24	25	26	27	Left side	Right side
S. fontinalis	50	...	15	13	9	5	4	2	2	...	...	...	...	...	17.7	18.4
C. namaycush	27	...	...	...	...	7	10	9	...	1	...	...	...	...	20.2	...
S. aureolus	16	1	4	1	2	3	1	2	...	1	1	...	...	...	18.6	...
S. oquassa	1	...	...	...	...	...	...	...	1	...	...	...	...	...	22.0	...
S. marstoni	38	...	...	...	2	5	13	12	5	1	...	...	...	...	20.4	...
S. alpinus	9	...	...	1	1	1	1	2	...	1	...	...	1	1	21.3	23.2

TABLE V. Variation with age in the total number of gill-rakers on the left side, in *S. fontinalis* from the same lake.

Fork length	N	Gill-rakers										Average
		11	12	13	14	15	16	17	18	19	20	
mm.												
45–60	10	1	...	...	2	4	3	...	...	...	...	14.7
148–218	10	...	...	...	...	...	5	3	1	1	...	16.8

TABLE VI. Number of vertebrae.

Species	N	Vertebrae										Average
		58	59	60	61	62	63	64	65	66	67	
S. fontinalis	13	2	5	4	1	1	...	...	...	...	...	59.5
C. namaycush	23	...	...	...	1	8	7	4	2	1	...	63.0
S. aureolus	18	...	...	...	1	3	2	5	7	...	...	63.8
S. oquassa	1	...	...	...	...	...	...	...	...	1	...	66.0
S. marstoni	30	...	...	1	1	1	5	13	7	2	...	63.9
S. alpinus	16	...	...	...	1	1	4	...	3	2	5	64.8

(*d*) *Number of vertebrae.* This is the most widely employed character. Although classical studies by Danish authors, especially that by Tåning (1952, p. 177), proved that the number of vertebrae could easily be influenced by temperatures in the process of the development of the embryo, the number of vertebrae is still commonly used. There are also difficulties in determining the first vertebra and separating the last vertebrae or "hypural".[5] Apparently

[5]Some authors, as Wilder (1952, p. 187), use the term "urostyle" instead of "hypural". Both terms anatomically are rather incorrect (see subsection "Caudal fin" below).

different authors did not include the same number of vertebrae in the hypural. As we shall see later on in the subsection "Caudal fin", in Salmonidae the last three vertebrae comprise the hypural. In Table VI all vertebrae were counted, including three of the hypural.

Among chars, only S. *fontinalis* has a decidedly smaller number of vertebrae (less than 60 on the average) than the rest of the group (Table VI). In the remaining species, vertebrae vary on the average from 63 to 65. As Table VII shows, the greatest differences are noted among the pre-caudal vertebrae.

TABLE VII. Number of precaudal and caudal vertebrae in different chars.

		Precaudal vertebrae						Caudal vertebrae			
Species	N	33	34–5	36–7	38–9	40–1	Average	23–4	25–6	27–8	Average
S. fontinalis	13	2	7	4	...	...	34.7	4	9	...	24.8
C. namaycush	13	...	...	...	5	8	40.0	11	2	...	23.7
S. aureolus	8	...	...	1	5	2	39.1	1	6	1	25.6
S. oquassa	1	...	...	...	1	...	39.0	...	...	1	27.0
S. marstoni	30	...	...	7	18	5	38.3	4	21	5	25.6
S. alpinus	18	...	...	3	8	7	38.9	1	11	6	25.9

(*c*) *Number of fin rays.* In the case of chars this character is of the least value. Tables VIII–XI present the data on this subject. In addition to small natural variations observed in the number of fin rays in different species, there are technical difficulties in counting small simple rays in front of the dorsal and anal fins. The best way is to remove the skin and stain the rays with alizarin. In larger specimens the stained fins should be dissected and made transparent by placing in glycerine. To avoid error in counting these small rays in unstained specimens, some authors, as Kendall (1914, p. 24), counted only "fully-developed" rays in the dorsal and anal fins. Unfortunately there is no definition of the term "fully-developed". Some other authors count only branched rays, which are plainly seen even without staining with alizarin. Unfortunately the number of branched rays in younger fish (parr) is smaller than in older individuals of the same species (Table X). In general, S. *fontinalis* has a somewhat smaller number of rays in all fins.

TABLE VIII. Number of rays in the dorsal fin.

		Branched rays						All rays					
Species	N	7	8	9	10	11	Average	9	10	11	12	13	Average
S. fontinalis	22	...	11	11	...	...	8.5	3	11	6	2	...	10.3
C. namaycush	19	...	4	12	3	...	9.0	...	2	8	4	...	11.1
S. aureolus	24	2	6	11	5	...	8.8	1	8	12	3	...	10.7
S. oquassa	4	...	...	2	2	...	9.5	...	...	...	1	...	12.0
S. marstoni	49	...	...	8	39	2	9.9	...	2	16	20	1	11.5
S. alpinus	17	...	1	8	7	1	9.5	1	4	6	6	...	11.0

TABLE IX. Number of rays in the anal fin.

Species	N	Branched rays					All rays					
		7	8	9	10	Average	8	9	10	11	12	Average
S. fontinalis	22	8	12	2	...	7.7	3	8	9	2	...	9.5
C. namaycush	19	...	3	14	2	9.0	...	...	2	12	...	10.9
S. aureolus	24	5	12	7	...	8.1	...	8	13	3	...	9.8
S. oquassa	4	...	...	4	...	9.0	...	...	...	1	...	11.0
S. marstoni	48	...	13	26	9	8.9	...	5	15	16	2	10.4
S. alpinus	18	1	12	5	...	8.2	...	8	7	3	...	9.7

TABLE X. Variation with the age in the number of branched rays in the dorsal and anal fins of *S. aureolus* from the same lake.

Fork length	N	Dorsal fin					Anal fin			
		7	8	9	10	Average	7	8	9	Average
mm.										
56–83	8	2	4	1	1	8.1	4	3	1	7.6
105–225	8	...	1	6	1	9.0	1	5	2	8.1

TABLE XI. Total number of rays in the ventral and pectoral fins on the left side.

Species	N	Ventral fin						Pectoral fin						
						Average							Average	
		8	9	10	11	Left side	Right side	11	12	13	14	15	Left side	Right side
S. fontinalis	24	21	3	...	...	8.1	...	1	3	18	2	...	12.9	...
C. namaycush	19	3	14	2	...	9.0	9.2	...	1	6	9	1	13.6	13.6
S. aureolus	24	4	14	4	2	9.2	8.5	1	...	6	13	1	13.6	13.6
S. oquassa	4	1	3	...	...	8.8	...	...	1	3	...	...	12.8	...
S. marstoni	47	13	34	...	...	8.7	8.9	5	8	20	14	1	13.0	12.8
S. alpinus	18	1	13	4	...	9.2	...	...	...	4	9	5	14.1	...

(*f*) *Number of pyloric caeca.* Although pyloric caeca are mentioned very seldom in current literature, in the opinion of the present author this is one of the most important taxonomic characters. Among chars, *C. namaycush* has an unusually high number of caeca (Table XII), which varies from 108 to 173. It is of interest to note that, according to Stokell (1951, p. 214), lake trout acclimatized in New Zealand retain an equally high number of caeca, which varies there from 128 to 164.

The remaining chars, with the exception of *S. aureolus*, have rather low caeca counts, the average being less than 40. The specimens of *S. aureolus* from Lake Sunapee present a very unusual situation. As Table XIII shows, there is a definite increase in the number of caeca with the age of the fish. In specimens

TABLE XII. Total number of pyloric caeca.

Species	N	Pyloric caeca												
		20-9	30-9	40-9	50-9	60-9	70-9	80-9	90-9	100-9	120-39	140-59	160-79	Average
S. fontinalis	30	2	15	13	...	...	...	...	...	...	...	...	...	38.4
C. namaycush	38	...	...	...	...	...	...	...	...	1	21	13	3	137.9
S. aureolus	35	...	14	14	1	3	2	...	1	...	...	...	...	45.9
S. oquassa	1	...	1	...	...	...	...	...	...	...	...	...	...	39.0
S. marstoni	34	1	21	12	...	...	...	...	...	...	...	...	...	37.7
S. alpinus	16	1	8	5	2	...	...	...	...	...	...	...	...	39.1

smaller than 36 centimetres, the number of caeca varies from 33 to 51 with an average of 42. The larger specimens have from 63 to 91 caeca, with an average of 72.5. This increase depends, however, not on the age of the fish, but rather on the possibility that older individuals are hybrids between *S. aureolus* and *C. namaycush*. This observation is supported by the fact that in the case of *Salmo salar*, which during growth passes from fresh to salt water, there is a very slight increase in the number of pyloric caeca in older specimens. The variations presented on Table XIII are caused most probably by the fact that the specimens of salmon studied were collected from widely separated regions.

TABLE XIII. Variation with size in the number of pyloric caeca.

Salmo salar			*Salvelinus aureolus*			*Cristivomer namaycush*		
N	Fork length	No. of caeca	N	Fork length	No. of caeca	N	Fork length	No. of caeca
	mm.			*mm.*			*mm.*	
	100	47.8		126	42.3		116	142.4
10	(53–145)	(33–61)	8	(79–175)	(34–51)	14	(82–198)	(108–173)
	449	53.5		304	42.0		225	131.8
2	(448–450)	(49–58)	6	(228–355)	(33–47)	10	(208–266)	(119–154)
	819	67.0		631	72.5		594	142.0
5	(678–1,147)	(59–74)	6	(530–695)	(63–91)	5	(515–650)	(128–155)

The smallest number of caeca was 20, which was found in a specimen of S. *alpinus* from Walton Lake, New Brunswick. This low value corresponds to that of S. *malma* from Kodiak Island, Alaska, reported by DeLacy and Morton (1942, p. 84).

SKELETON

Among the different skeletal parts of chars so far studied by us, the most important sections are the *tail* and *skull*.

(*a*) *Caudal fin*. Several papers dealing with the caudal skeleton have been published. Among more recent ones should be mentioned publications by Hollister (1936) and Ford (1938), containing a good list of references. Unfor-

tunately neither of these dealt with Salmonidae. Looking through bibliographies, one wonders if anything had been published on that subject during the last century. As a matter of fact, apparently Kölliker (1859) was the last author who studied to some extent the caudal skeleton in Salmonidae, particularly that of *Salmo salar*.

In the near future we are planning to publish a separate paper dealing with the caudal skeleton in Salmonidae. Therefore, it is sufficient to give here only the most important findings, which are illustrated by Figures 2 and 3. Several skeletal structures are very important from the taxonomic point of view. In naming them, we followed closely the terminology used by Hollister (1936, pp. 258–260) for Isospondyli other than Salmonidae.

(1) *Centrum* is the central element of a vertebra on which the neural and haemal processes are formed.

(2) *Covering bony plate* is the term proposed by Kölliker (1859). According to Goodrich (1909, p. 102) this plate could be a modified neural arch. As this term does not indicate clearly the position of this bone, we think that the name *caudal bony plate* would be more appropriate. This bone, *c.b.p.* is a very important part of the skeleton in Salmonidae (Fig. 2, 3).

(3) *Epurals* (2 or 3 in Salmonidae) are bones dorsal to the urostyle and supporting caudal fin rays.

(4) *Expanded haemal processes* are on the ventral surface of vertebral centra.

(5) *Expanded neural processes* are on the dorsal surface of vertebral centra.

(6) *Hypurals* (7 in Salmonidae) are the bones ventral and posterior to the urostyle, supporting the caudal fin rays. In taxonomic papers the term "hypural" or "hypural plate" is used rather loosely. For instance, according to Rounsefell and Everhart (1953, p. 411), it is "a flattened plate to support the rays of the caudal fin, that may be formed from one or more vertebrae". In the case of Salmonidae, we found that it includes the three last centra and urostyle, for definition of which, see below.

(7) *Uroneurals* (2 pairs in Salmonidae) are the only paired bones, directed upward and backward on the lateral and dorsal surfaces of the urostyle. They protect the lower end of the urostyle. The members of each pair of uroneurals are found on the left and right sides of the tail.

(8) *Urostyle* is the posterior terminal segment which follows the last undoubted centrum. In Salmonidae the urostyle remains non-ossified. In some taxonomic works, as that by Clothier (1950, p. 11), it is defined as "the fan-like tail segment articulated with the last true vertebra". This last definition of the urostyle is not applicable at all to Salmonidae.

The most important structures are: the caudal bony plate, the expanded neural and haemal processes, and the uroneurals. Table XIV summarizes these differences in the various species of chars. It is of interest to note that in Coregonidae and in *Salmo gairdneri* there are *three epurals*, while in *S. salar* and all eastern chars there are only *two*.

TABLE XIV. Details of the caudal fin skeleton in Salmonidae.

Character	*S. fontinalis*	*C. namaycush*	*S. aureolus*	*S. marstoni*	*S. alpinus*	*Salmo salar*
C.b.p.[a] shape	fan-like, broad and short	crescent-like, narrow and long	fan-like, broad and long	crescent-like, narrow and long	crescent-like, narrow and long	fan-like, broad and long
Number of centra covered by c.b.p.	3	4	$3\frac{1}{2}$	$3\frac{1}{2}$	$3\frac{1}{2}$	$3\frac{3}{4}$
Number of expanded haemal processes	6	5	7	6	5	4
Number of expanded neural processes	5	6	7	4	5	4
Shape of 2nd uroneural	narrow and short	broad triangle	broad triangle	narrow and long	narrow and short	Very narrow and long (sabre-like)
2nd uroneural / 1st uroneural	1/2	3/4	1/2	4/5	1/2	3/4

[a]C.b.p.—caudal bony plate.

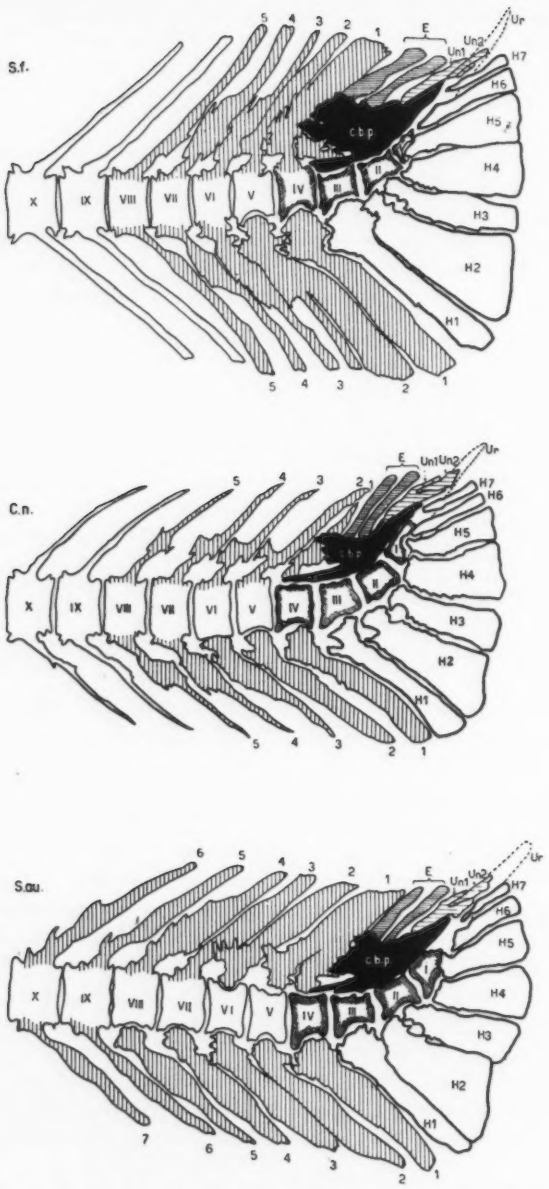

FIGURE 2. The caudal skeleton in three species of chars: *Salvelinus fontinalis, Cristivomer namaycush* and *Salvelinus aureolus*. Roman numerals (I–X) refer to the last ten centra. Arabic figures (1–7) refer to expanded processes either haemal or neural: c.b.p.–caudal bony plate; E–epurals; H_1–H_7–hypurals; Un_1 and Un_2–first and second uroneurals; Ur–urostyle.

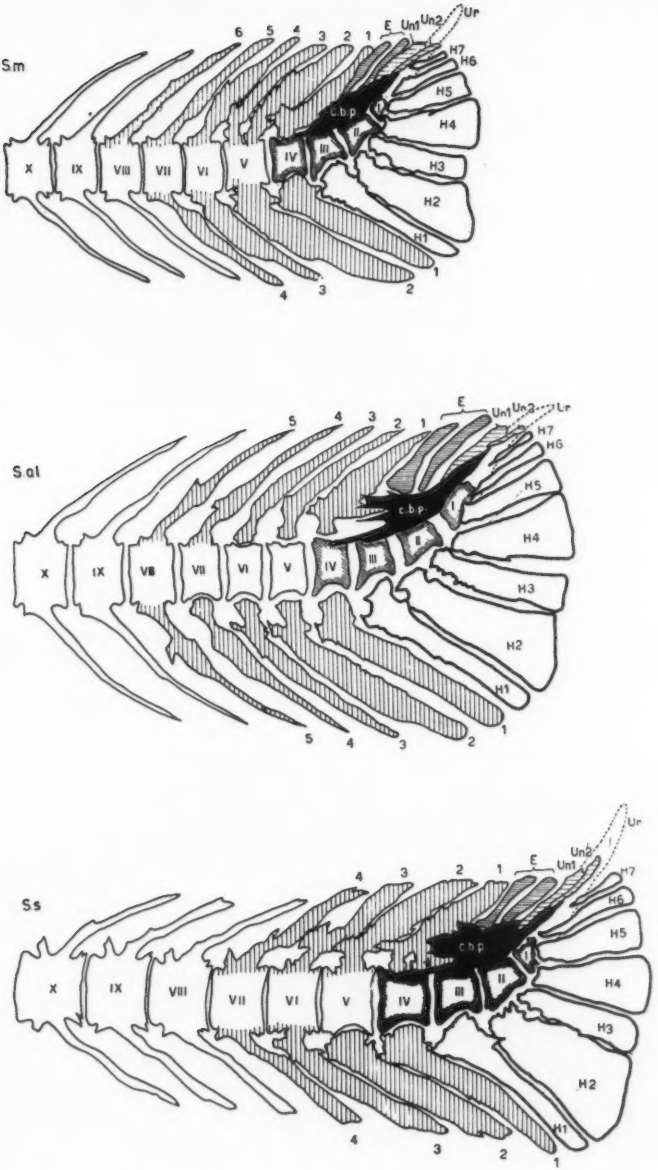

FIGURE 3. The caudal skeleton in three species of Salmonidae: *Salvelinus marstoni*, *S. alpinus* and *Salmo salar*. For explanation of symbols see Figure 2.

(*b*) *Skull.* The skeleton of fish heads have been described by numerous authors. Gregory (1933, pp. 152–154) in his important work treated the skulls from a broad point of view of comparative anatomy. He illustrates only, however, the *Salmo* sp., without giving details of any one particular species. Tchernavin in several papers (1918, 1938) has masterfully dealt with changes in the skull of *S. salar* and of species of *Oncorhynchus*. On the other hand, the skull of different chars has received little attention. The work by Richardson (1836), with its beautiful lithographs, is probably the last paper on the subject. It is rather unfortunate that these illustrations, made from dry skulls, resulted in the omission of several important details.

For the present paper we have had time to study in detail and draw skulls of only *C. namaycush* and *S. marstoni*. We have followed the terminology used by Tchernavin (1938) for *S. salar* (Table XV). The most important peculiarities are in the shape of the *praeoperculum*, the *jugal* and the lower (3rd) *orbital*. There is also a difference in the distance between the praeoperculum and the postorbitals (Fig. 4, 5).

TABLE XV. List of abbreviated designations used for membrane bones in the skull of chars. The terminology after Tchernavin (1938, pp. 167–168).

A	Articular	O^4	Suborbital posterior
An	Angular	O^5	Postorbital lower
Br	Branchiostegals	O^6	Postorbital middle
D	Dentary	O^7	Postorbital upper
F	Frontal	Opc	Opercle
IO	Interoperculum	P	Pterotic (squamosal)
J	Jugal	Pm	Praemaxillary
M	Maxillary	PO	Praeoperculum
N	Nasal	Q	Quadrate
Na	Nasal cartilage	Sc^1	Sclerotic anterior
O^{1-7}	Orbitals	Sc^2	Sclerotic posterior
O^1	Supraorbital (Lacrimal)	SEt	Supra-ethmoid
O^2	Praeorbital	SO	Suboperculum
O^3	Suborbital anterior	Sp	Supra-operculum

TABLE XVI. Teeth on the tongue (*supralingual*) in Salmonidae.

No.	Species	FL[a]	Sex	Tongue		
				Length	Width	Number of teeth[b]
		mm.		*mm.*	*mm.*	
6	*S. salar*	990	♀2	38	14	4 + (5) = 9
2,518	*S. fontinalis*	419	♂1	22	9.5	11 + (0) = 11
2,900	*S. aureolus*	695	♂4	28	11	8 + (6) = 14
2,911	*C. namaycush*	648	♂4–5	27	12	8 + (10) = 18

[a]FL—fork length.
[b]In parentheses are indicated numbers of alveoles from which teeth have been lost.

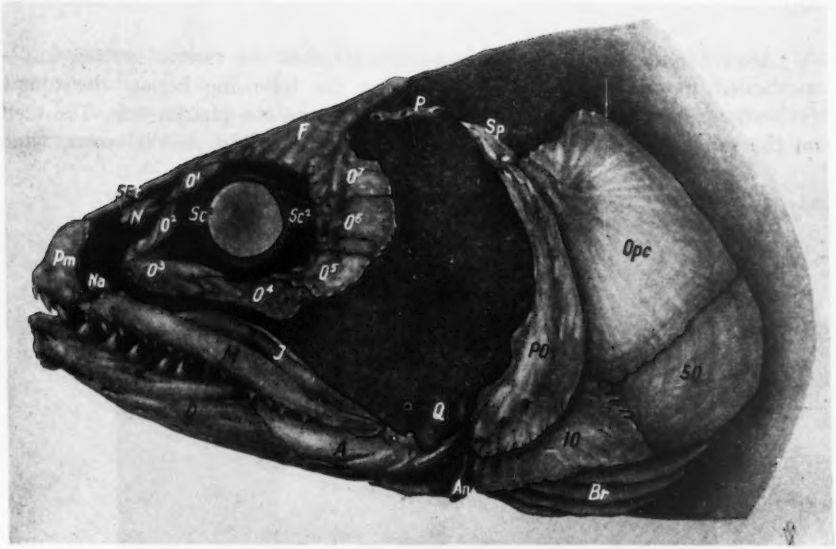

FIGURE 4. Lateral view of the skull of an adult male *C. namaycush* showing membrane bones. For explanation of designations see Table XV. The head length of this specimen is 14 centimetres.

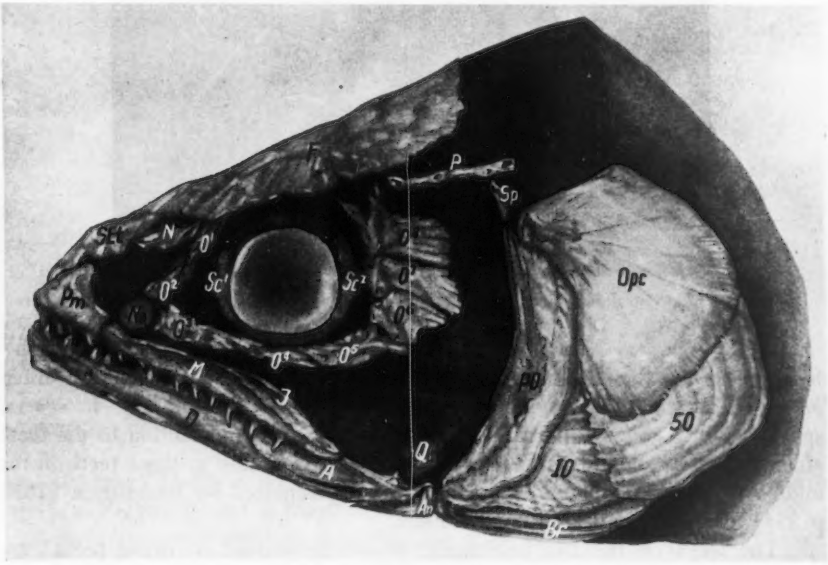

FIGURE 5. Lateral view of the skull of an adult male *S. marstoni* showing membrane bones. For explanation of designations see Table XV. The head length of this specimen is 6 centimetres.

Among inner structures, which are characteristic for various species, can be mentioned the differences in the teeth on the following bones: the tongue (*supralingual*), the vomer, the basi-branchials[6] and the pharyngeals. The teeth on the tongue in *C. namaycush* are typically located in parallel rows, while

FIGURE 6. Floor of mouth of a spawning female of *C. namaycush*. The head length is 17 centimetres.

in other species they are formed in a triangle (Fig. 6–9). There is also a difference in the number of teeth present on this bone (Table XVI). In several specimens of S. *marstoni* from Lake Harriman, Gaspé, in addition to the teeth along the lateral edges of the tongue, we found from one to three teeth in the middle of the supralingual, a condition already reported by Richardson (1836, p. 174) for his S. *hoodi* from Boothia Felix.

The teeth on the basi-branchials, commonly known as "hyoid teeth", are absent in S. *fontinalis*, but developed in the remaining chars. It is of interest to note that Stokell (1940) observed hyoid teeth in some specimens of S. *fontinalis*

[6]These bones are more often, although incorrectly, called *hyoids* (see Kendall, 1914, p. 11).

acclimatized in New Zealand. He was good enough to send us three of these specimens.[7]

In *C. namaycush* and *S. aureolus*, the hyoid teeth are strongly developed and form a broad patch. In the remaining species they are either in single or

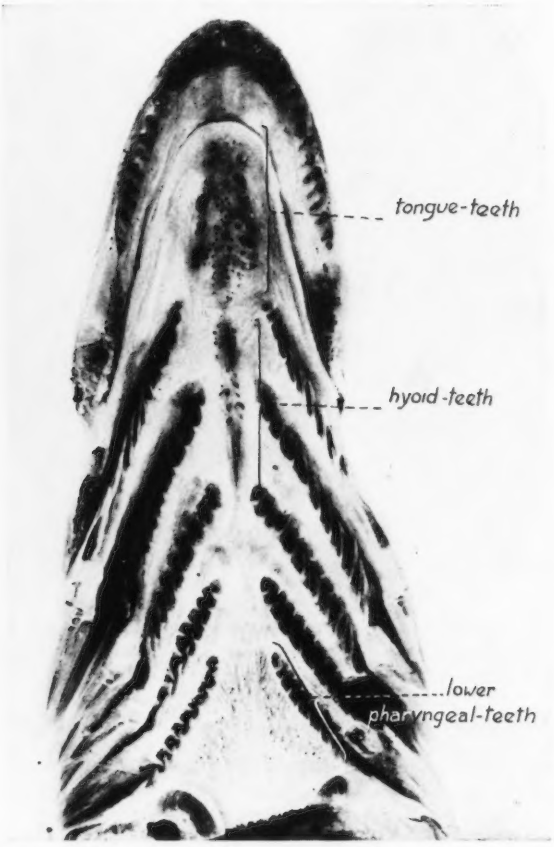

FIGURE 7. Floor of mouth of a spawning female of *S. marstoni*. The head length is 6 centimetres. The specimen was stained with alizarin, therefore teeth appear black on the photograph.

double rows. There is no doubt that each species possesses its own type of teeth, as Figures 10 and 11 illustrate.

Preliminary observations show that the pharyngeal teeth (upper and lower) are helpful also in separating certain species of chars. Further details will be given in a separate paper.

[7]A preliminary examination suggested that these specimens are most probably hybrids between *S. fontinalis* and *S. alpinus*.

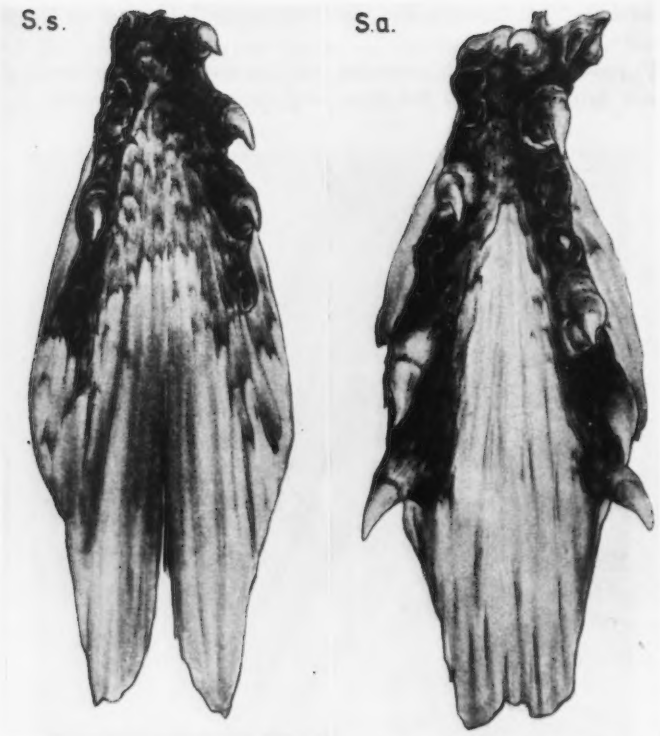

FIGURE 8. The dorsal view of the tongue (*supralingual*) with teeth in two species of Salmonidae: *Salmo salar* and *Salvelinus aureolus*. Magnified 3 and 4 times, respectively. Other details are given in Table XVI.

COLORATION

The colour pattern of chars should be treated according to the stage of development of the fish.

(*a*) *Parr*. The average number of vertical dark bars on the sides of young fish varied from 9 in *S. fontinalis* to 12 in the case of *S. marstoni* and *S. alpinus*. Table XVII gives details on this subject. The incomplete bars were included in our counts.

(*b*) *Adults*. The coloration of different chars is very characteristic. Table XVIII contains data on this subject.

(*c*) *Spawners*. During the spawning season both sexes acquire a special livery. While females in *S. fontinalis* and *C. namaycush* change only slightly, in the remaining chars they are nearly as brightly coloured as the males. Table XVIII summarizes other details.

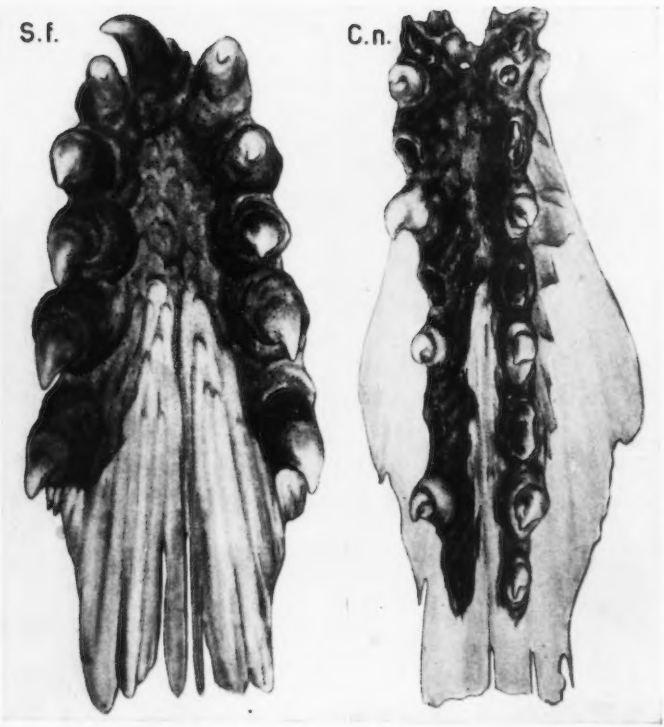

FIGURE 9. The dorsal view of the tongue (*supralingual*) with teeth in two species of char: *S. fontinalis* and *C. namaycush*. Magnified 3 and 4 times, respectively. Other details are given in Table XVI.

TABLE XVII. Number of parr markings on the side of young fish. (The incomplete bars are included in the counts.)

Species	N	Number of bars									Average
		7	8	9	10	11	12	13	14	15	
S. fontinalis	20	1	5	8	5	1	...	...	...	...	9.0
C. namaycush	16	...	...	7	4	5	...	...	...	...	9.9
S. aureolus	6	...	...	...	...	2	4	...	...	...	11.7
S. marstoni	9	...	...	...	1	...	5	2	...	1	12.3
S. alpinus	10	...	...	...	...	4	2	3	...	1	12.2

SEXUAL DIMORPHISM

The male char, regardless of species, on reaching sexual maturity acquires the secondary sexual dimorphism. These characters are particularly well developed in older individuals.

FIGURE 10. The dorsal view of the basibranchial with "hyoid teeth" in a spawning male of *C. namaycush*. The overall length of this bone is 23 millimetres; smaller figure on lower right shows its lateral view.

FIGURE 11. The dorsal view of the basibranchial with "hyoid teeth" in a spawning male of *S. marstoni*. The overall length of this bone is 10 millimetres; smaller figure on upper right shows its lateral view.

(*a*) *Permanent dimorphism.* In the case of males, the greater length of the pectoral and ventral fins and that of the maxillary are included in this category.

(*b*) *Seasonal dimorphism.* During spawning, males acquire a hook on the lower jaws, an increase in body depth and nuptial livery. All these characters disappear gradually after reproduction. The most striking differences between sexes are observed in *S. fontinalis*, *S. aureolus* and *S. alpinus* (see Sprules, 1952, p. 9). On the other hand, in *C. namaycush* and *S. marstoni* even during spawning the sexes are hardly distinguishable. Upon completion of our studies on char skulls, we probably shall find some changes in them relating to the sexual dimorphism, as Tchernavin (1938) found for salmon.

(*c*) *Pearl organs.* These organs, so characteristic for Coregonidae in breeding season, never have been reported for Salmonidae. Among chars, only *C. namaycush* of both sexes have them (Fig. 12). We shall give more details on the structure and findings of pearl organs in lake trout in a separate paper.

Weight

There is a pronounced distinction in the size and weight among grown-up individuals of different chars. *S. marstoni* and *S. oquassa* are small, seldom

Figure 12. Anal fin section of a spawning male of *C. namaycush*. Scales over the lower portion of the fish clearly exhibit pearl organs. The base of the anal fin is 54 millimetres long.

TABLE XVIII. Types of coloration in different chars.

Type	*S. fontinalis*	*C. namaycush*	*S. aureolus*	*S. oquassa*	*S. marstoni*	*S. alpinus*
			BOTH SEXES			
Red spots on sides	large, rather few, typically encircled in blue	absent	replaced by small orange spots	replaced by very small orange spots, rather numerous	replaced by very small orange spots, rather numerous	replaced by a few orange spots, rather large
Small whitish round spots on sides and back	absent	present	present	present	present	?
Vermiculations on back	well-developed	present	present	absent	absent	absent
Black stripe on lower fins	present	absent	absent	absent	absent	absent
			SPAWNING MALES			
Sides	red	yellow or faintly pinkish	carmine or orange	carmine (?)	carmine	carmine (?)
Lower fins	red with black stripe and white front margin of average width	yellowish or pale pinkish, with white circles and narrow white margin	carmine with broad white margin	orange with white margin of average width	orange with white margin of average width	orange with white margin of average width
Lower surface of head	black	white	blackish	white	white	?
Tips of both jaws	black	white	carmine	?	carmine	carmine
Roof of mouth	black	white	blackish	white	white	white

weighing more than a pound. S. *fontinalis* can reach over 7 or 8 pounds. S. *aureolus* often weighs from 9 to 11 pounds. S. *alpinus*, the anadromous form, can attain 20 and even more pounds. The giant among chars is *C. namaycush* which can tip the scales at more than 40 pounds.

Habitat

Some chars, such as S. *fontinalis* and S. *alpinus*, can be found in both fresh and salt water. The remaining four species are strictly freshwater forms. *C. namaycush* and S. *aureolus* are lake forms which spawn there too. S. *oquassa* and S. *marstoni*, although lake dwellers, spawn typically in brooks.

Number of Chromosomes

Attempts have been made already to use the number of chromosomes in different species of fishes for taxonomic purposes. Several papers dealing with this subject have been published. One of the most recent authors is Svärdson (1945), who not only studied the problem critically, but presented an exhaustive bibliography on the subject.

Using dissected embryos or testicles on smears, fixed in acetocarmine, Svärdson (1945) determined the number of chromosomes in Salmonidae and related families. According to him, the number of chromosomes varied as follows in different species from Sweden:

Species	*Diploid number of chromosomes*
Salmo salar	60
S. trutta	80
Salvelinus alpinus	80
S. fontinalis	84
Coregonus lavaretus	80
C. albula	80
Thymallus thymallus	102
Osmerus eperlanus	58

In addition, there are differences in the shape of certain chromosomes. Moreover, the hybrids are distinguished from the parent species by a different diploid number of chromosomes and by marked meiotic disturbances.

Thus, when the technique of chromosome study is more widely used, it will become, no doubt, a useful tool in taxonomic studies on Salmonidae.

Hybrids

In Canadian literature the finding of natural hybrids between different species of chars has never been mentioned. Nevertheless, there is always the possibility of finding them. On the other hand, during recent years, several hybrids have been produced artificially in hatcheries. In Quebec, L. R. Seguin, Director, Station piscicole des Cantons de l'Est, succeeded in obtaining fertile hybrids between *C. namaycush* and several other species. In New Hampshire, Dr. B. W. Corson, Chief of Fisheries Division, Fish and Game Department,

Concord, was equally successful in the hybridization of S. *aureolus* and other chars. Our Laboratory possesses several valuable samples of these hybrids of the first and second generations.

Our interest in these hybrids is mainly from a taxonomic point of view. By the study of these hybrids, we can see clearly that the typical characters of different chars are dominant at least in the first generation. For instance, the black stripe on the lower fins in S. *fontinalis* and the high number of pyloric caeca in *C. namaycush* are predominant.

CONCLUSIONS

In spite of the fact that our study is not complete as yet, some definite conclusions can be drawn.

1. Among meristic characters, the number of pyloric caeca is very important.
2. Body proportions and meristic characters other than pyloric caeca seldom are adequate to properly describe a species of char.
3. The details of char skeletons, particularly of the tail and head, are very important taxonomic characters, sufficient in themselves to define a species.
4. The following relationship can be presented as a tentative arrangement for chars:

(*a*) *C. namaycush* represents a distinct genus, which can be characterized by peculiarities of membrane bones of its skull, the shape of the vomer, the unique arrangement of the teeth on the tongue, details of the tail skeleton, the high number of pyloric caeca, and the presence of pearl organs during spawning time.

(*b*) S. *fontinalis* represents a distinct subgenus *Baione*, established in 1842 by De Kay. Its main characters are: the presence of a little-forked tail, black stripe on lower fins, the absence of hyoid teeth, and an uninterrupted row of vomerine and palatine teeth (see also Vladykov and McKenzie, 1935, p. 56). For true-to-nature colour illustrations of wild speckled trout, see Vladykov (1953). For more details on meristic characters in the native S. *fontinalis*, see Wilder (1952). Fuster de Plaza (1950, pp. 45–55) gave information on meristic characters and body proportions of S. *fontinalis* acclimatized in Argentina.

(*c*) The remaining species are included in a subgenus *Salvelinus*, established in 1836 by Richardson. The relationship between individual species is as follows:

S. *aureolus* is a distinct species, quite different from the rest of the chars. Other information on this species is given by Vladykov and Corson (1953, MS). Sisson (1950, pp. 529–536) published coloured photographs of this species.

S. *marstoni* and S. *oquassa* are very close to each other, possibly belonging to the same species. Everhart (1950, p. 242) presented some new data on S. *oquassa* and in another paper (1950a p. 27) published a colour photograph of it.

S. alpinus represents a very complex group, which in Canada consists of two or possibly more species. These forms can be separated by the differences in the skeleton, body proportions and meristic characters. Vladykov (1933, pp. 19–20) pointed out the existence of anadromous and land-locked forms of the Arctic char in the Hudson Bay region. Grainger (1953) dealt with the biological aspects of this char from Baffin Island. Walters (1953, p. 258) reported a considerable variation in the spacing between the vomerine and palatine teeth in Arctic char from Western Canada. Good colour photographs of European chars were published by Alm (1942, pp. 616–627) and Hansen (1948, pp. 624–626).

5. Material available now for fish studies is preserved in either alcohol or formalin. Unfortunately such specimens cannot be used satisfactorily for the preparation of skeletons. To clean properly the bones of Salmonidae and Coregonidae, the specimens should be either fresh, preserved in salt, or frozen. Thus in the future, the institutions and organizations interested in studies of fish should collect and keep frozen specimens. This frozen material, as a necessary complement to regular fish collections, would bring new possibilities to research.

6. Taxonomic studies not only are of a theoretical significance but have considerable practical value. The Salmonidae and Coregonidae are two of the most valuable groups of Canadian fishes. The classification of both depends on the knowledge of the same characters. The taxonomy of these groups is extremely involved and time-consuming. It would be essential, therefore, to establish a research centre, a kind of "Salmon Institute", where several specialists could co-operate in their studies. Only by co-ordination can we hope that a definitive classification of salmonoid fishes will be eventually accomplished.

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The drawings for this paper were done most expertly by Mr. P. I. Voevodine, Quebec.

To all these persons, the author wishes to extend his most sincere thanks.

RÉSUMÉ

Pour la présente étude, quelque 300 spécimens furent examinés. Ils appartenaient aux espèces suivantes: *Cristivomer namaycush*, *Salvelinus fontinalis*, *S. aureolus*, *S. oquassa*, *S. marstoni* et *S. alpinus*. Pour distinguer les espèces, les caractères numériques et les proportions du corps sont en général moins importants que le squelette. Cependant le nombre d'appendices pyloriques est assez significatif. Les détails du crâne et du squelette de la queue sont surtout utiles pour la taxonomie. En plus des spécimens de Salmonidés conservés en formaline ou en alcool, il sera nécessaire à l'avenir de garder des poissons congelés ou salés, afin de faciliter la préparation du squelette.

Outre la livrée nuptiale, qui apparaît chez tous les Salmonidés durant la fraye, seuls les *C. namaycush* des deux sexes portent alors des tubercules cornés sur les écailles.

Les relations taxonomiques provisoires entre les différentes espèces peuvent être résumées de la façon suivante: *C. namaycush* représente un genre distinct; *S. fontinalis* appartient au sous-genre *Baione*, et les autres espèces peuvent être groupées dans le sous-genre *Salvelinus*. Il est presque certain que *S. alpinus* se présente au Canada au moins sous deux formes différentes.

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The Oxygen Supply to Salmon Eggs in Spawning Beds[1,2]

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ABSTRACT

By using standpipes set 12 inches into the stream bottom the oxygen content and apparent velocity of the gravel water in the controlled-flow section of Nile Creek were observed. Values of dissolved oxygen content and velocity that just supply the full oxygen demand of salmon eggs were defined. The high mortalities of chum salmon eggs in the pre-eyed stage, that have been found in certain areas, may be explained on the basis that oxygen demands of 0.00013 to 0.0003 mg./egg/hr. at temperatures of 0.1° to 8.2° C. were not being met, owing to very low oxygen content or very low apparent velocity of the water in the gravel. Values as low as 0.2 p.p.m. and 2 mm./hr. were recorded. A portable gravel-water sampler is described, which can be used (1) to obtain samples of subsurface water for the determination of dissolved oxygen; and (2) to calculate apparent velocity of gravel water from rate of dilution of an added dye.

CONTENTS

Introduction	933
Part I. Evaluation of Oxygen Supply at Nile Creek	937
Determination of oxygen requirements of pre-eyed chum salmon eggs	937
Determination of oxygen content and velocity of gravel water	940
Development of formula equating oxygen demand and supply	943
Discussion	944
Part II. A Gravel-water Sampler for Spawning Ground Surveys	947
Description	947
Calibration	949
Summary	951
Acknowledgments	952

INTRODUCTION

In a study of the freshwater survival of the chum salmon (*Oncorhynchus keta*) at Nile Creek on Vancouver Island (Neave, 1947) high losses, averaging 70%, have been found in the pre-eyed stage of the eggs. The present paper records an attempt to determine whether these losses could have been due to lack of oxygen.

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In the writings of Hata (1931), Hewitt (1931), Hubbs, Greeley and Tarzwell (1932), Schaeperclaus (1933), Hobbs (1937, 1940, 1948), Cameron (1939, 1941), White (1942), Shaw and Maga (1943), Shetter, Clark and Hazzard (1946), Moffett (1949) and Vibert (1950) there is ample evidence that an improvement of the quantity and quality (oxygen content, temperature, freedom from silt and chemicals) of the water supply usually improves the survival of naturally or artificially incubated salmonid eggs.

Shaw and Maga found a tendency for undeveloped eggs to resist decomposition in troughs of gravel, apparently due to a protective coating of silt. The same effect has been noted in the controlled-water section of Nile Creek (Wickett, 1952), where eggs, planted the previous year, have been found preserved (but of course dead) in the gravel after twelve months. The composition of the stream bottom in one such area was of consolidated large stones, small gravel, sand and silt, and the surface flow was good with little surface silting. In another of these areas the surface was covered with six inches of sand and silt. In contrast, excellent survival was found in an area where there was reduced surface flow and much surface silting, but a spring upwelled through loose gravel. In view of this, surface silt of itself did not seem to be lethal, but in certain circumstances it would appear that the circulation of the water is so greatly reduced that there is insufficient oxygen for the survival of living eggs or for the disintegration of dead eggs in the gravel.

Hobbs (1937) recognized the desirability of an exact study to determine whether eggs in natural redds receive sufficient oxygen to keep them alive. His statement of the problem specified data on the oxygen consumption of the eggs, the oxygen content of the water and data on the hydraulics of the redd such that the velocity of the water passing through it could be calculated. However, Rose (1945), who has formulated the laws of flow of fluids through granular materials, states that the calculation of exact velocities in a particular part of gravel bed is virtually impossible.

In Part I of this paper, the evaluation of the oxygen supply to pre-eyed chum salmon eggs on the controlled-water section of Nile Creek (Fig. 1) is considered in three sections: (1) field determinations of the oxygen consumption were made in static volumes of water, (2) a method of measuring flow 10 to 12 inches below the stream bed was devised and data on the oxygen content and velocity of water in the gravel gathered, and finally (3) a formula equating oxygen demand and supply was derived.

In Part II a gravel-water sampler is described, by means of which surveys of natural spawning grounds can be made, to find whether the oxygen supply in them is sufficient to keep salmon eggs alive.

The following symbols are used:

A = oxygen demand of the eggs, i.e., the amount of oxygen necessary for normal metabolism, in mg. O_2/egg/hr., assumed to be the same for all eggs of similar past history at a given temperature and at a similar stage of development. Oxygen consumption may be less than the demand.

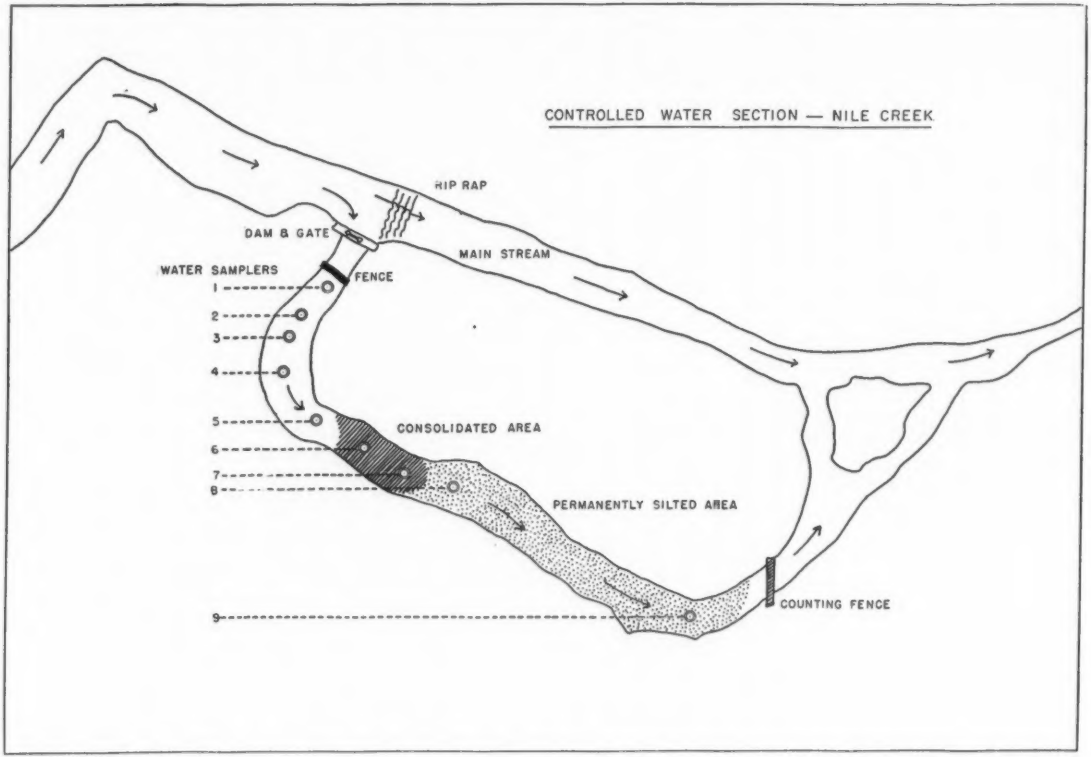


FIGURE 1. Map of controlled-water planting bed at Nile Creek. The 350-foot section was formed by damming the stream and clearing an old channel.

R = radius of egg, in mm.
DO = amount of oxygen dissolved in water, in mg. O_2/litre.
C = critical value of DO, below which A is reduced.
n = number of eggs in a horizontal row in the direction of water flow.
a = area at right angles to flow of water which supplies oxygen-bearing water to eggs.
u = component of true velocity in direction of flow, in mm./hr.
v = apparent velocity of water through gravel, i.e.,

$$\frac{\text{volume discharge per unit time}}{\text{cross-sectional area of gravel bed}}$$

Amplifying notes on certain of the symbols follow.

For eyed *Salmo salar* eggs the oxygen consumption increases with age and temperature (Hayes, 1949), but is independent of the amount of oxygen dissolved in the water, provided the dissolved oxygen (DO) is above a critical value (C). The oxygen consumption is reduced when the amount of oxygen dissolved in the water is reduced below this critical value.

For eggs without circulation under the capsule, the critical value of dissolved oxygen varies with the oxygen demand of the egg, the square of its radius and the rate of diffusion of oxygen through the egg (Krogh, 1941). It may be expressed in terms of oxygen tension, i.e., partial pressure of oxygen in millimetres of mercury multiplied by the percentage saturation; in terms of atmospheres, i.e., fractions of 760 mm. Hg. pressure of oxygen; as the degree of oxygen saturation of the water; or simply as parts per million at a given temperature. The last is used here for ease of application in field studies.

Krogh shows that aquatic eggs larger than 1 mm. in diameter must have a low metabolic rate to be able to survive when depending on diffusion alone to supply sufficient oxygen. Therefore the developmental stage of salmonid eggs just before the establishment of the circulatory system is a most critical one. The embryo is developing to a considerable size with a correspondingly increasing oxygen demand. Anything in the environment that delays the establishment of the circulatory system disproportionately, for example an adverse temperature history (Hayes, Pelluet and Gorham, 1953), leaves the embryo particularly vulnerable to a lowered oxygen supply. It may well be that both the critical and the lethal oxygen tensions rise together until the laying down of the circulatory system (approximately the eyed stage). At that time both values will drop. The critical tension increases with age, but the lethal level of dissolved oxygen for hatching chum eggs and alevins is close to 2 p.p.m. at 5° C. (unpublished data of D. R. Alderdice, J. R. Brett and W. P. Wickett). Their results show that the larva has a zone of resistance in which the metabolic demand can be reduced. The most obvious change is the greatly reduced activity of the heart. The pre-eyed egg has no such activity to reduce and is wholly dependent on diffusion to supply its needs. Hence Harvey's (1928) formula in Krogh (1941) is used to calculate the critical oxygen value (C) for pre-eyed eggs.

The true velocity (u) of fluids in gravel beds is impossible to determine.

Nominal or apparent velocity (v) is the figure used to describe the speed of water flowing through gravel and is defined as the volume discharge per unit time (Q) divided by the total cross-section of the area (a) through which the fluid is assumed to flow, just as though this area were filled with water only, i.e.,

$$v = \frac{Q}{a}$$

In the case of a clear area, $v = u$. If a fluid discharges through a porous medium, and discharge (Q) and area of cross-section (a) are the same as for the clear area, then u is greater than v, for Q is coming from only the total area of the pores in a. Using the dimensions of length and time

$$v = \frac{L^3/T}{L^2} = L/T$$

The porosity of gravel is defined as the volume of pores divided by the sum of the absolute volume of gravel plus the volume of pores.

Part I. Evaluation of the Oxygen Supply at Nile Creek

DETERMINATION OF OXYGEN REQUIREMENTS OF PRE-EYED SALMON EGGS

Methods

Nineteen glass-top preserving jars of approximately 950 cc. volume were weighed dry and filled with water at 6° C. to determine their volumes to ± 0.5 cc. Each top and bottle was numbered and used together. Eggs were placed carefully in the jars by means of "egg pickers", and the jars were filled with water which was led to the bottom of the jar by a tube from the hatchery head trough at the Nile Creek field station. The jars were capped without air bubbles and placed in the head trough so that they were covered with water. A water seal and a fairly uniform known temperature were thus obtained.

Owing to the extreme susceptibility of pre-eyed eggs to shock, the water over these eggs could not be stirred. In most cases, 100 eggs were used as a sample as they formed a single layer on the bottom of the jar, although samples of 50 and 200 eggs were used occasionally.

Oxygen determinations were made on samples of water taken at the time of filling. Procedures and equipment for oxygen determination are described by Tully (1949, 1950). At intervals varying from one to 150 hours, jars were opened carefully and water drawn off by siphon from the bottom of the sealer for the final oxygen determination. The oxygen sample bottle (300 cc.) was rinsed once, the sample for determination being the second volume taken off.

To find out if excessive amounts of carbon dioxide were being formed, the pH of the water from some of the bottles was taken by a Beckman meter at the end of the experiment. The range found was 6.89 to 7.1, which was within the normal range of the natural waters.

After making the oxygen determination, the eggs were dried by rolling them in cheesecloth and then on filter paper, live and dead were counted, weighed,

and their volume determined by displacement. The radius of the eggs (R) was found by measuring a row of ten eggs. The oxygen consumption for later stages of development of chum, pink and coho eggs were measured as a check on the correct order of magnitude of oxygen demand.

Results

Results are given in Table I.

Oxygen consumption of the eggs was calculated as follows:

$$A = \frac{(V_B - V_F)(DO_1 - DO_2)}{1000\,NT}$$

where A = oxygen consumption of the eggs, in mg. O_2/egg/hour
V_B = Capacity of bottle, in cc.
V_F = total volume of eggs, in cc.
DO_1 = dissolved oxygen in water at start of experiment, in mg./l.
DO_2 = dissolved oxygen in water at end of experiment, in mg./l.
N = number of eggs used
T = duration of experiment in hours.

$(DO_1 - DO_2)$ is divided by 1000 to convert mg./l. to mg./cc.

The biochemical oxygen demand (BOD) of the water was found to be nil, but the BOD of dead chum eggs at 0.1°–0.7° C. was found to be about the same as the consumption of living eggs. As the time of death of eggs in the experiment was not known, corrections were not made for the BOD after death of eggs.

Critical values of dissolved oxygen (C) were not found for pre-eyed eggs as the value of DO could not be reduced to this limit within the time of the experiment (152 hours). To obtain an approximate value for pre-eyed eggs, the formula of Harvey (1928) quoted by Krogh (1941) was used, as it gave reasonable checks with both the faintly-eyed chum and Lindroth's (1942) data.

Harvey assumed that the egg is a homogeneous spherical body in which oxygen is used up at a constant rate, the same throughout, and that the oxygen tension at the centre is maintained at zero. (Oxygen tension is the product of percentage oxygen saturation and the partial pressure of oxygen in air saturated with water vapour at 760 mm. Hg.) Oxygen consumption is calculated for the eggs as a whole, rather than for the embryo only. The suitability of this procedure is indicated by Krogh (1941, p. 53).

Harvey's formula for eggs without circulation under the capsules is:

$$C_0 = \frac{A.r^2}{6D} \text{ atmospheres}$$

where C_0 = critical concentration of oxygen in atmospheres (760 mm. Hg) at the surface of the egg.
A = oxygen consumption in ml./g./min.
r = radius of egg in cm.
D = diffusion coefficient of oxygen within the egg in ml./cm./cm.^{2}/min. per atmosphere of difference in oxygen tension. Assumed to be 0.0000126 (Hayes *et al.*, 1951).

TABLE I. Oxygen consumption of pre-eyed chum salmon eggs determined in static water, and comparative values of consumption and critical dissolved oxygen for other eggs.

State and age of eggs at start		Consumption A	Critical DO C		Temperature	No. of eggs and replicates	
			Exptl.	Calc.[a]			
	days	*mg./egg/hour*	*p.p.m.* O_2	*p.p.m.* O_2	° C.		
			Oncorhynchus keta, chum salmon				
Pre-eyed	0	0.00013	...	0.72	3.7–5.2	100	(11)
"	5	0.0003	...	1.67	8.0–8.2	100	(3)
"	12	0.0002	...	1.14	0.1–0.7	100	(9)
" dead		0.0003	...	...	0.1–0.7	40	(6)
Faintly eyed	67	0.0002	...	...	0.1–0.7	100	(5)
" "	85	0.00079	<5	3.7	3.6–4.9	50	(13)
10 days before hatching	103	0.0002	...	...	5.9–6.1	200	(4)
			O. gorbuscha, pink salmon				
Faintly eyed	26	0.0003	...	...	6.2–6.9	100	(1)
Eyed	33	0.0006	...	...	7.9–8.3	100	(3)
7 days before hatching	48	0.0007	...	...	7.9–8.3	100	(3)
7 days alevin	62	0.01	...	...	8.0–8.2	50	(3)
			O. kisutch, coho salmon				
Faintly eyed	67	0.0002	...	...	0.1–0.7	100	(5)
Hatching	110	0.003	...	...	4.3–4.9	10	(8)
0 day alevin	110	0.009	...	...	4.3–4.9	10	(1)
			Salmo salar, Atlantic salmon (Lindroth, 1942)				
"Domed"		0.00014	0.76	1.1	5.5	...	
Brain just developed		0.00028	...	...	4	...	
		0.00068	...	...	13	...	
Nearly hatching		0.0039	5.8	...	5	...	
Hatching		0.0067	10	...	17	...	
			S. salar, Atlantic salmon (Hayes *et al.*, 1951)				
Eyed	25	0.00104	3.1	...	10	...	
Hatching	50	0.0048	7.1	...	10	...	
			O. masou, Japanese salmon (Kawajiri, 1925)				
Pre-eyed		0.001	...	...	?	...	

[a]Calculated from Harvey's (1928) formula, in Krogh (1941).

The following procedure was followed to change from C_0 (expressed in atmospheres) to C (expressed in p.p.m.). To convert to mm. of Hg, C_0 must be multiplied by the barometric pressure (760 mm.). The partial pressure of oxygen (P_0) (approx. 157 mm.) must be divided into this figure to give the equivalent degree of saturation of oxygen. Then the degree of saturation value is multiplied by the p.p.m. oxygen required for full saturation at the given temperature (DO_s).

The critical value of DO is expressed thus: $C = \frac{760Ar^2DO_s}{6DP_0}$ p.p.m.

The formula given in Tully (1950) is used to get a factor (approx. 0.7) to convert mg./l. to ml./l. O_2. The weight of a chum egg is 0.29 g. approximately. Calculation of the first three values of C shown in Table I was as follows:

1. Pre-eyed chum eggs; age 0 days; temp. 3.7°–5° C.; A = 0.00013 mg./egg/hr.

$$A = 0.00013 \text{ mg./egg/hr.} = \frac{0.00013 \times .71}{.28 \times 60} = 0.0000055 \text{ ml./g./min.}$$

$$C = \frac{760 \times 5.5 \times 10^{-6} \times 1.6 \times 10^{-1} \times 12.8}{6 \times 1.26 \times 10^{-5} \times 157.5} = 0.72 \text{ p.p.m. } O_2.$$

2. Pre-eyed chum eggs; age 5 days; temp. 8° C.; A = 0.0003 mg./egg/hr.

$$A = 0.0003 \text{ mg./egg/hr.} = \frac{0.0003 \times .72}{.26 \times 60} = 0.0000138 \text{ ml./g./min.}$$

$$C = \frac{760 \times 1.38 \times 10^{-5} \times 1.6 \times 10^{-1} \times 11.9}{6 \times 1.26 \times 10^{-5} \times 157.2} = 1.67 \text{ p.p.m. } O_2.$$

3. Pre-eyed chum eggs; age 12 days; temp. 0.1°–7° C.; A = 0.0002.

$$A = 0.0002 \text{ mg./egg/hr.} = \frac{0.0002 \times 0.7}{0.30 \times 60} = 0.0000078 \text{ ml./g./min.}$$

$$C = \frac{760 \times 7.8 \times 10^{-6} \times 1.6 \times 10^{-1} \times 14.4}{6 \times 1.26 \times 10^{-5} \times 157.9} = 1.14 \text{ p.p.m. } O_2.$$

DETERMINATION OF OXYGEN CONTENT AND VELOCITY OF GRAVEL WATER

Methods

The gravel-water data were gathered on a side channel which has been dammed and a water gate installed so that the water flow may be controlled (Wickett, 1952). In this section freshly fertilized ova have been planted each fall since 1947. Apparent velocity, oxygen content and temperature data were gathered here (Fig. 2, 3).

Nine 1½-inch pipe rail fittings, known as "cross with side outlet" were fitted with ½-inch pipe 24 inches long in the side outlet, forming a standpipe with a 300-cc. reservoir, having four 4.5 cm. lateral openings at the base (Fig. 4). These pipes were wrapped in wire mosquito netting and set 12 inches into the gravel along the centre of the controlled-water planting bed. The third one of the series was modified so that a recording thermometer bulb could be placed in it. A second thermograph was set up to record surface temperature. Temperatures were measured in the other pipes by thermometer. Samples of water were taken by suction for oxygen determinations according to the method outlined by Tully (1949, 1950) (cf. Cole, 1932).

Dye was used to find the rate of sub-surface flow. Both eosin and methylene blue were used, but the methylene blue proved more satisfactory. Dye was added by pipette to the pipe, the water stirred and a sample taken. After several hours

FIGURE 2. Photograph of controlled-water section looking downstream. Standpipes at No. 2, 3 (thermograph) and 4 position are visible.

FIGURE 3. Photograph of controlled-water section looking upstream. Standpipes at No. 8A, 8, 7, 6, 5 positions are visible. Stream bottom in foreground is heavily silted.

a second sample was taken. The samples were compared with standard concentrations to determine dilutions. The standard series of dyes was made up by taking one volume of concentrated dye and adding an equal volume of water, one volume of this diluted dye was used as the first of the series, the remainder had one volume of water added and half of the second dilution became the second of the series, etc. (Dilutions halfway between those above may be useful.) Each standard was equivalent to the previous one with an equal volume of clear water added to it. The number of volumes added per hour was calculated by dividing the difference on the scale of the two samples by the number of hours the dilution had been taking place. A photoelectric colorimeter was used as well, but it was not convenient for field work. A more stable dye than methylene blue would be desirable.

FIGURE 4. Fixed standpipe used to sample water 12 inches down in gravel of controlled-water section.

Volumes per hour were converted to apparent velocity (v) by calibrating the pipe in a trough of gravel (see page 949).

In the planting bed, the upper quarter was loose gravel, free of sand "normal" (pipes #1–5), the second quarter consolidated gravel (low porosity) (#6, 7), and the lower half covered with a heavy layer of sand and leaf material (#8, 9). The second quarter had the steepest gradient whereas the lower half was nearly flat.

During July and August 1949 the planting bed was loosened by digging and hosing. On February 22–23, 1950, the bed was covered with fine sand experimentally.

Results

OXYGEN CONTENT OF GRAVEL WATER. Average values of oxygen saturation have varied from 56 to 88 per cent in the normal gravel (#1–5). Low values (less than 8%) were found in the consolidated portions just before digging and hosing (#6, 7). Zero and near zero values were found in the permanently silted portion (#8, 9).

RATE OF SUB-SURFACE FLOW. The rate of flow of the water beneath the channel was found to be closely related to the discharge in the main stream when the surface flow was kept constant (Fig. 5). The average apparent velocity varied from 5 to 36 mm./hr. (0.4 to 2.8 ft./day).

TEMPERATURE. A comparison of the thermograph records for pipe #3 (normal gravel) and the surface, show that the temperatures tend to be similar between six and nine o'clock in the morning when the surface water is coldest, but the gravel water lags up to 18 hours in reaching diurnal maxima. Temperature differences between surface and gravel waters were least at the upper end of the planting bed, near the inlet end at the highest level, and greatest in the lower half which is nearly level and permanently silted (#8, 9). Differences in temperature tend to be associated with lowered oxygen saturation, but not with rate of sub-surface flow.

EFFECT OF DIGGING AND HOSING GRAVEL. Washing the stream bed silted up the pipes at first, but after the pipes were also cleaned out, the average values of dissolved oxygen were raised, particularly in the consolidated area. This previously consolidated area maintained a high saturation value (78–95%) for a year. The silted area was raised from near zero to 45 per cent but reverted to low values in two months. The thermograph records show that the lag in diurnal temperature maxima became zero to 6 hours in the consolidated area, as compared with up to 18 formerly. This effect lasted for ten weeks.

EXPERIMENTAL SILTING. Silting the bed experimentally caused no immediate change in the oxygen content of the water but the average apparent velocity was reduced by half, in spite of an increase in surface flow.

DEVELOPMENT OF FORMULA EQUATING OXYGEN DEMAND AND SUPPLY

The oxygen supply to eggs in water will depend on the volume of water per unit time (Q) delivering oxygen to the eggs, and the oxygen per unit volume (DO) dissolved in the water; i.e., gross supply is QDO. The oxygen available for full metabolism will consist of the dissolved oxygen in excess of the critical oxygen content; i.e., the effective supply is

$$Q(DO - C) \qquad (1)$$

Acceptable conditions for full metabolism will obtain when the weight of oxygen per unit volume, in excess of the critical weight per unit volume, multiplied by

the volume per unit time equals or is greater than the weight of oxygen required per unit time, i.e.,

$$A \leq Q(DO - C) \tag{2}$$

Assume as a first approximation that if the oxygen-supplying area (a) presented by an egg to the flow of water is known, then Q may be calculated from

$$Q = va$$

Oxygen diffuses very slowly through water over distances above a few millimetres. Let the distance at right angles to the flow of water that oxygen will diffuse during the time the water is passing an egg be x mm. (Krogh, 1941).

For a single egg, a will be $\pi(R + x)^2$ and the supply of oxygen is

$$\pi(R+x)^2v(DO-C)10^{-6}\text{mg.O}_2\text{/egg/hr.} \quad (x \text{ probably} \leqslant 1 \text{ mm.}) \tag{3}$$

For eggs in an egg mass, without any admixture of gravel, a, the area of egg, plus interstitial space per egg, presented in one plane is a hexagon, so the maximum supply in this case is

$$2\sqrt{3}R^2v(DO-C)10^{-6}\text{mg.O}_2\text{/egg/hr} \tag{4}$$

In expression (4) no allowance is made for a progressive decrease of DO as the water passes successive layers of eggs. In order that the last or nth egg normal to the direction of water flow, shall just receive sufficient oxygen, then the oxygen supply must be equal to n times the demand of one egg, or, the demand of one egg equals $1/n$ times the supply.

If the oxygen demand, the critical value of dissolved oxygen, and the radius of the eggs is known, the sufficiency of the oxygen supply to an egg mass in the gravel may be estimated from the apparent velocity and oxygen content of the water in the gravel, using this formula:

$$nA \leqslant 2\sqrt{3}R^2v(DO-C)10^{-6} \tag{5}$$

DISCUSSION

The results for the oxygen demand of pre-eyed chum salmon eggs (Table I) are not precise but are field determinations which establish the order of magnitude. Their general agreement with Lindroth's and Hayes's results leads to the belief that they may be used in the formulae developed above to establish minimum values of velocity and oxygen content necessary to supply the full demand of the eggs.

The standpipes at Nile Creek do not give a full coverage of the controlled-water section nor were the readings taken consistently enough to evaluate the entire bed's oxygen supply during the pre-eyed stage. However they permit the following conclusions.

The supply of water to gravel one foot below the surface, is derived from surface flow and from sub-surface flow of water (of lowered oxygen content) from the banks. (On another portion of the main stream, a spring at the edge of the creek had an oxygen content of 47–54%.) When the main stream rises, there

is increased sub-surface flow from the water table on either side of the stream bed (Fig. 5) (see also Hoyt, 1942). The surface contribution will vary with the depth of the surface water and the permeability of the surface gravel. The permeability of the surface gravel varies with the presence or absence of silt and the degree of consolidation (porosity).

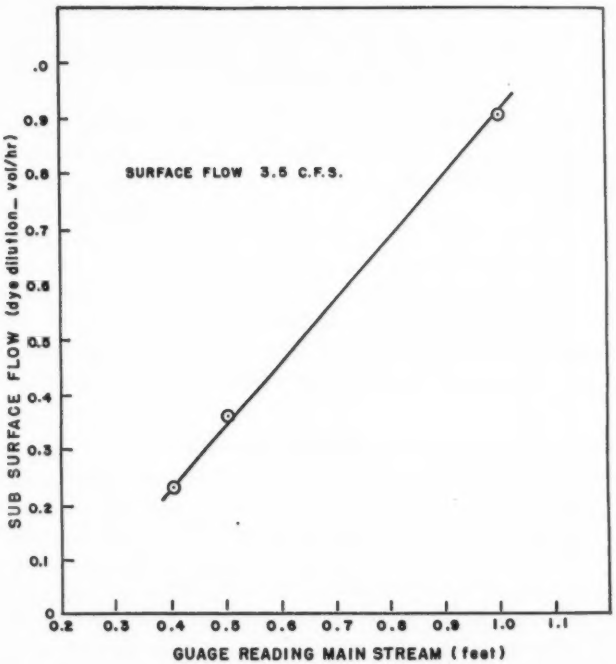


FIGURE 5. Relation between sub-surface water flow 12 inches under controlled-water section and main stream gauge readings. Surface flow on controlled-water section was kept constant at 2 inches on a weir. Sub-surface flows are average readings of all standpipes. They may be converted to apparent velocity using Figure 8. The sub-surface flow varies with changes in discharge of the main stream outside the controlled-water side channel.

Certain values of dissolved oxygen and apparent velocity are compared with a curve of limiting values that just maintain full metabolism of pre-eyed eggs (Fig. 6).

In expression (5) A, R, C, are constants for eggs of a given age and at a given temperature; v and DO are variables. If the oxygen supply just equals the demand, then expression (5) is the equation of the positive values of a hyperbola of the form $v(\mathrm{DO} - \mathrm{C}) = \mathrm{K}$ (a constant); this is the curve of limiting values of v and DO. At any point above or to the right of the curve the oxygen supply exceeds the particular oxygen demand being considered. At any point

below or to the left, the full demand is not being met, probably with fatal results.

Using the values A = 0.0003 mg./egg/hr., R = 4 mm., C = 1.67 p.p.m. 0_2, for $n = 1$, expression (5) reduces to $v(DO - 1.67) = 5.5$, and for $n = 10$ to $v(DO - 1.67) = 55$. The asymptotes of both these curves are $v = O$ and $DO = 1.67$.

In Figure 6 there are plotted several points well to the left or below the curve of limiting values. Dead eggs from the previous year's planting have been found in these areas. Those points with DO < C indicate that there are portions of the controlled-water section in which the full oxygen demand of pre-eyed chum eggs

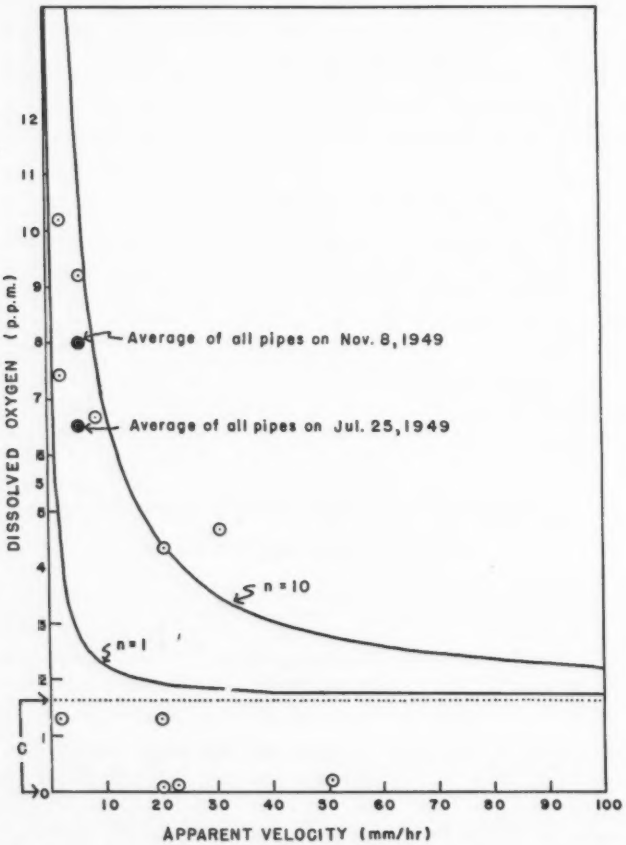


FIGURE 6. Curve of limiting values of dissolved oxygen and apparent velocity of water to supply the full oxygen demand of a single pre-eyed chum salmon egg at 8° C. (n=1), and a line of ten eggs at the same temperature (n=10). For values to the right and above the curve, supply exceeds demand; below and to the left, supply is less than demand. Some low values found in the gravel of the Nile Creek controlled-water section are plotted as open circles.

cannot be met irrespective of velocity. These readings (DO < C) were gathered in the heavily silted part of the bed. Thousands of chum eggs planted there died after the original silting occurred. If the major cause of egg mortality in the gravel is lack of oxygen then high survival rates should be associated with points above and to the right of a curve similar to that in Figure 6 and low survival rate associated with points to the left of and below it. Experiments are being carried out to establish directly the form of the curve given in Figure 6.

Part II. Development of a Gravel-Water Sampler for Spawning Ground Surveys

To survey spawning grounds, values of dissolved oxygen and velocity are required from individual redds since both the author and Cameron (1939, 1941) have found that samples of eggs from redds show either high or low survival rather than an intermediate condition.

The fixed "railing-pipe" standpipes set in the stream had the advantage of giving a fair-size volume of ground water for sampling dissolved oxygen. Dye samples when taken with a glass pipette required the removal of no more than 5 cc. so that the hydraulic disturbance was minimal. For general survey purposes a portable sampler was required that could be driven into the stream bottom anywhere desired. Ruggedness and simplicity were necessary.

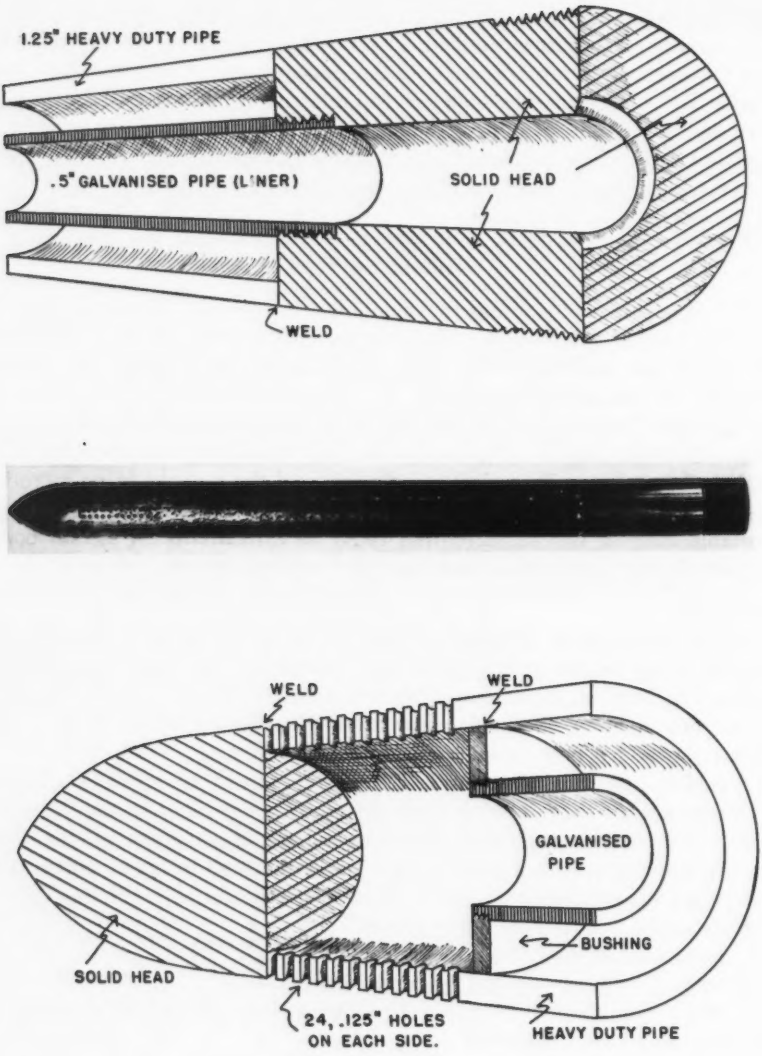
Description

At first a *well point*, commonly available in hardware stores, was modified by blanking all but the lower inch of the perforations. This pointed perforated pipe was found to break at the threads after being driven into the gravel a few times. After experimentation, the model illustrated (Fig. 7) was made of heavy duty 1¼ inch pipe and has been found satisfactory.

A rubber gasket is fitted inside the driving cap to minimize the influx of surface water while the sampler is being driven by sledge-hammer into the gravel. A half-inch pipe liner welded into the tube reduces the stagnant volume of dye when determining apparent velocity of flow. Perforations in the chamber at the bottom allow the sub-surface water to flow through the chamber, diluting the dye.

The sampling procedure suggested is:

1. Rinse sampler free of sand and dye.
2. Screw on driving cap and tighten by hand.
3. Drive the sampler to a standard depth (say 10 inches) keeping the perforations in a known direction.
4. If sand is handy, pour it around the pipe to reduce exchange of surface water next to the pipe. Remove the cap and note the time taken for the water to rise to stream level. The ease of driving the sampler and the time for filling may give a general description of the permeability of the gravel.
5. If the water in the sampler is cloudy, draw off by suction several volumes until it clears. Take a sample for oxygen determination and place a thermometer in the sampler. Harper's (1953) semimicrodetermination of dissolved oxygen is recommended.



GRAVEL-WATER SAMPLER

FIGURE 7. Gravel-water sampler. *Above,* section of head; *below,* section of tip; *middle,* outside appearance without cap. After driving the sampler into the gravel to a known depth, a water sample is withdrawn by suction for oxygen determination. Apparent velocity is found by comparing the rate of dilution of a dye, introduced into the chamber, with a standard series of dilutions.

6. Fix the water sample for oxygen determination.

7. Take the temperature.

8. By means of a length of narrow bore (approx. ⅛ inch) glass tubing, pipette concentrated dye into the sampler. Stir, stop the top of the glass tube, insert to the bottom and open the top of the tube so as to take dye sample from the bottom of the sampler.

9. Stop the top of the tube, remove from the sampler and compare the dye sample with a standard series (see page 942) in test tubes made of the same tubing as the pipette. Note the reading.

10. Titrate the oxygen sample.

11. In a quarter of an hour take another dye sample from the bottom of the sampler. A longer period or a more finely graduated standard dye series may be necessary to get a change in the reading.

Calibration

DISSOLVED OXYGEN. The sampler was driven 12 inches into the gravel 6 inches from each of the set pipes in the controlled-water section at Nile Creek and dissolved oxygen determinations made on samples from each (Table II). The greatest difference noted, 1.0 p.p.m., was found where the dissolved oxygen in the fixed pipes was less than one part per million. The sampler was left 4 days and the difference became 0.4 p.p.m. If the sampler is cleared of clouded water and the dissolved oxygen saturation not very low, oxygen determinations can be made within an hour. The sampler should be left in the gravel for several days if accurate readings are required at points of low oxygen saturation.

VELOCITY. A trough was made of 2×12 inch planks 6 feet long. Screens were set in it and the volume between them filled with gravel from Nile Creek to give a bed 113 × 22 × 25.5 cm. and head and tail water pools at either end of the gravel bed. Water was lead into the head water pool, where the water was maintained at a constant level by an overflow set so that there was no surface flow over the gravel. The outflow was a tap set in the centre of the end wall of the tail water pool. Samples of water were collected from the tail water, measured by volume and time to determine the rate of flow at the beginning and end of each test.

One of the standpipes was set 12 centimetres into the centre of the gravel bed, and the procedure for obtaining the dilution of dye outlined above was followed for various rates of flow. The apparent velocity was calculated by dividing the discharge (cc./hr.) by the cross-section of the bed (561 sq. cm.). Dye dilution is reported in equal volumes of water added per hour (vol./hr.).

For some of the tests, the "fixed" standpipe was set with two of the openings in line with the direction of flow and in others, 45° off the line of flow.

The uncompacted porosity of the dry gravel bed in the trough was 23%. The porosity of samples from Nile Creek was 22%.

The results are shown in Figure 8. It appears the sampler gives promise as a means of evaluating the dissolved oxygen content and apparent velocity of gravel

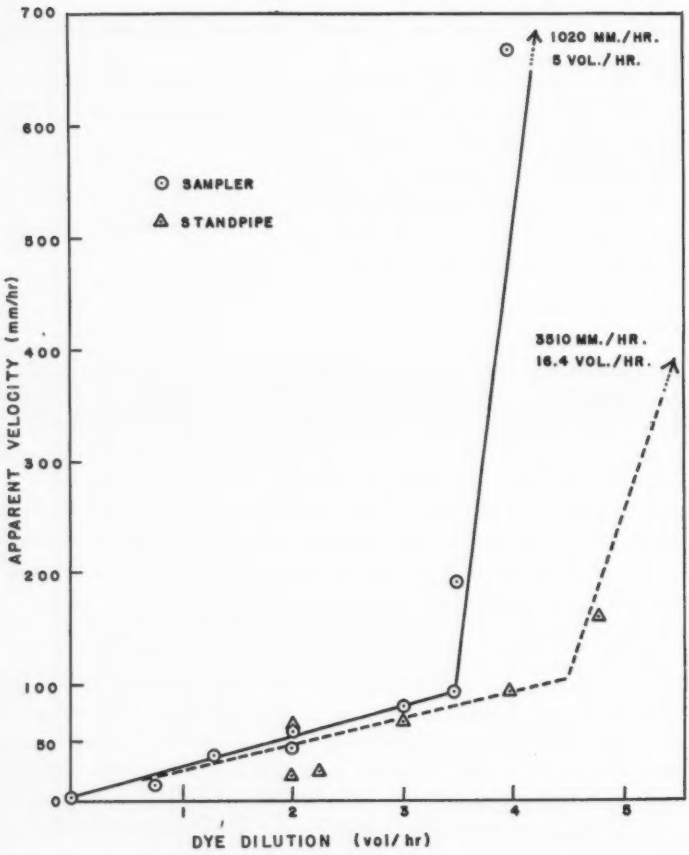


FIGURE 8. Calibration of standpipe and sampler for apparent velocity. Velocities were calculated from discharges through a trough of 561-sq. cm. cross-section, containing gravel. Velocities encountered in nature were below the inflection points. Average maximum (untamped) porosity was 23%.

TABLE II. Calibration of sampler for dissolved oxygen. Water samples were taken by sampler 6 inches away from standpipes in Nile Creek controlled-water section.

	Temp.	DO	Difference	Time to fill sampler
14.43, June 30, 1950	° C.	*p.p.m.*	*p.p.m.*	*minutes*
Surface	12.5	10.6		
Standpipe 8B	11.1	0.4		
Sampler	11.1	2.3	+1.9	4½
11.40, July 4, 1950				
Surface	11.8	10.6		
Standpipe 8B	11.2	0.13		
Sampler	10.2	0.54	+0.4	...
14.00, July 4, 1950				
Surface	12.9	10.4		
Standpipe 4	12.6	5.2		
Sampler	12.5	5.3	+0.1	2½
10.50, July 5, 1950				
Surface	11.8	10.9		
Standpipe 2	11.8	6.7		
Sampler	11.8	6.25	−0.5	4
Surface	11.8	10.9		
Standpipe 1	11.8	9.8		
Sampler	11.8	8.9	−0.9	2
09.53, July 6, 1950				
Surface	11.8	10.8		
Standpipe 5	11.8	8.5		
Sampler[a]	12.0	8.5	0	...
11.10, July 6, 1950				
Surface	11.8	10.8		
Standpipe 6	12.0	10.1		
Sampler[b]	12.0	10.0	−0.1	...
11.25, July 11, 1950				
Surface	11.0	11.0		
Standpipe 7	10.8	9.6		
Sampler	10.8	9.8	+0.2	...

[a]Sampler in gravel one hour. Four volumes discarded to clear water.
[b]First sample used; water clear.

water. It should be calibrated in the type of gravel to be sampled. Tests of this nature are in progress.

SUMMARY

1. The oxygen demand of pre-eyed chum salmon eggs was found to be between 0.00013 and 0.0003 mg./egg/hr. at temperatures of 0.1°–8.2° C.

2. By means of standpipes set in the gravel, the oxygen content and apparent velocity of water was observed 12 inches below the surface of the gravel.

3. Theoretical limits of dissolved oxygen content and apparent velocity that just supply the full oxygen demand of salmon eggs were developed (Fig. 6).

4. Portions of the controlled-water section at Nile Creek were found in which there was an insufficient supply of oxygen to supply the demand of pre-eyed eggs. This may explain the high pre-eyed mortalities found in these areas.

5. A portable gravel-water sampler is described (Fig. 7), for determining the oxygen content and apparent velocity of gravel water.

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Studies of the Trematode *Stephanostomum baccatum* (Nicoll, 1907): I. The Distribution of the Metacercaria in Eastern Canadian Flounders[1]

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ABSTRACT

Stephanostomum baccatum, an acanthocolpid trematode, encysts during its larval stage in eastern Canadian flounders, the most consistently and heavily infected species being the winter flounder, *Pseudopleuronectes americanus* (Walbaum). The infection is heaviest in Passamaquoddy Bay. Hosts are usually more heavily infected in inshore than in offshore waters. Infections are light in the Bras d'Or Lakes and the northern Gulf of St. Lawrence. Larger fish have heavier infections than smaller fish. *S. baccatum* infects both European and North American flounders; two of its hosts occur on both sides of the Atlantic: the witch, *Glyptocephalus cynoglossus* (L.), and the American plaice (European long rough dab), *Hippoglossoides platessoides* (Fabric.).

INTRODUCTION

Stafford (1904) first identified metacercarial cysts from the winter flounder, *Pseudopleuronectes americanus* (Walbaum), in Passamaquoddy Bay, N.B., as the larval species *Stephanostomum hystrix* (Dujardin, 1845). Studies of this parasite by the author (Wolfgang, 1954) show it to be the metacercaria of *S. baccatum* (Nicoll, 1907). During an investigation of the life cycle of this parasite the author had the opportunity to examine, in a preliminary way, the incidence of the metacercarial cyst in all six species of eastern Canadian flounders.

MATERIALS AND METHODS

Most of the data concerning the behaviour and distribution of *S. baccatum* were collected at St. Andrews, N.B., in Passamaquoddy Bay. The winter flounder is the common flat fish in this bay and only limited information could be obtained here concerning the other species of flatfish which serve as hosts. Consequently, a number of trips to Nova Scotia and New Brunswick fishing ports were arranged during the summer of 1951 to examine offshore and inshore commercial landings of flatfish to determine the incidence of *S. baccatum* for a variety of species (see Fig. 1). These examinations were supplemented by reports of field technicians as well as by samples supplied by the Newfoundland Fisheries Research Station, St. John's, Newfoundland, and the United States Fish and Wildlife Stations at Boothbay Harbour, Maine, and Woods Hole, Mass.

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Two types of infection are encountered in flounders: cutaneous infections which show up on the fins and skin, and subcutaneous infections which are confined to the myotomes and pterygiophoral muscles. Both cutaneous and subcutaneous cysts are small, 0.2–0.5 mm. in diameter. They are either colourless or of the colour of the host muscular connective tissue, and are easily removed from the flesh by forceps.

Fish were first measured, then the entire surface examined for cutaneous cysts. Subcutaneous cysts are not always easy to see in large fish. The most efficient method was to hold the fish with the ventral surface toward the observer so that light shining through the fish would show them up as small opaque dots. When necessary, these were dissected out to confirm their identity. When identification of the cysts as *S. baccatum* was doubtful, samples were returned to the laboratory and the dissected larvae examined microscopically.

Four terms were used consistently to indicate the degree of infection, namely: "none"–no cysts visible, "few"–one to ten cysts, "numerous"–many scattered cysts, and "heavy"–concentrated masses of cysts usually along the base of the fin rays. The terms "numerous" and "heavy" are closely related.

CANADIAN FLOUNDERS AS HOSTS OF *STEPHANOSTOMUM BACCATUM*

Pleuronectid fish infected with the metacercariae of *S. baccatum* are found in all offshore and inshore waters of the Canadian Maritimes. The smooth flounder, the brill and the winter flounder are seldom, if ever, found offshore. The plaice, witch and yellowtail are mostly taken offshore, but are frequently found in large numbers in inshore waters, especially along the northern coast of Nova Scotia, as in Chedabucto Bay and the Bras d'Or Lakes (Martin, 1948).

Observations on the distribution and degree of infection in flounders are shown in Tables I to IV. Whenever possible exact locations, depths and dates of collection are included; blank spaces indicate that such data were not available.

Plaice. *Hippoglossoides platessoides* (Fabric.) (Table I)

Distribution: Entire coast, Arctic to Long Island. Smooth bottom–sand and mud–inshore and offshore. Most important flounder commercially; average commercial size 20 inches and two to three pounds; may reach 30 inches and seven pounds.

Sampling Depths: 15 to 125 fathoms.

Infection: Heavier inshore than offshore.

Infection Characteristics: Cysts in peripheral muscles and deeper in fillet muscles, (myotomes) in small fish. Cysts in fins when infection is "heavy".

Witch. *Glyptocephalus cynoglossus* (L.) (Table II)

Distribution: Entire coast, Newfoundland to Delaware Bay. Soft bottom–muddy, sand and clay–generally offshore. Commercial size about 18 inches and 1.5 pounds but can reach 25 inches and four pounds.

Sampling Depths: 10 to 155 fathoms (most common flounder in depths over 100 fathoms).

Infection: Heavier inshore than offshore.

Infection Characteristics: Yellow or cream-coloured cysts in pterygiophoral muscles, sometimes in fins. Transparent to white in young fish.

TABLE I. Distribution and degree of infection in plaice.

Location	Depth	Date	Total No. fish examined	Percentage infection			
				None	Few	Numerous	Heavy
	fathoms						
Baie des Chaleurs, N.B.		July 13, 1951	100	99	1	0	0
Orphan Bank	40–50	July 10, 1951	200	98	2	0	0
Bras d'Or Lakes, N.S.	3–10	June 21, 1951	100	100	0	0	0
Edge of Sydney Ground, N.S.		June 26, 1951	200	74	24	2	0
Tignish, P.E.I.		July, 1951	21	48	44	8	0
Petit de Grat, N.S.		July, 1951	50	48	44	4	4
Inshore Canso, N.S.		June 20, 1951	75	47	47	6	0
Offshore Canso, N.S.	69–72	June, 1951	94	0	70	27	3
Chedabucto Bay, N.S.	15–20	June 20, 1951	100	8	39	50	3
Shelburne Harbour, N.S.	Shoal	July, 1950	25	10	90	0	0
Passamaquoddy Bay, N.B.	10–20	Summer, 1950	14	1	61	15	23
Passamaquoddy Bay, N.B.		Summer, 1951	88	30	51	14	5
Small Point, Me.		June, 1951	40	20	80	0	0
Offshore samples							
Grand Bank	35–40	June 29, 1951	199	90	10	0	0
Banquereau		July 4, 1951	54	94	6	0	0
Sable Island	42–60	June 28, 1951	50	80	14	6	0
Newfoundland							
Inshore Newfoundland	140	July 10, 1951	60	62	37	1	0
Cabot Strait	124	Oct. 12, 1951	40	90	10	0	0
Notre Dame Bay	112		72	90	10	0	0

TABLE II. Distribution and degree of infection in witch.

Location	Depth	Date	Total No. fish examined	Percentage infection			
				None	Few	Numerous	Heavy
	fathoms						
Chedabucto Bay	10–12	June 20, 1951	168	65	33	2	0
Sable Island	42–60	June 28, 1951	100	87	13	0	0
St. Pierre Bank	115	July 3, 1951	82	97	3	0	0
Cabot Strait	155	Oct. 12, 1951	20	65	35	0	0

Small samples of 10 to 15 witch were found to be uninfected at Orphan Bank, Grand Bank, the northern Gulf of St. Lawrence and offshore from Canso. In 1950 one specimen with a "numerous" infection was reported from Passamaquoddy Bay. Dr. E. D. Premetz of the Fish and Wildlife Service, Woods Hole, Mass., reported (personal communication) a witch sample from Grand Manan Island in the Bay of Fundy heavily infected with cysts resembling those of *S. baccatum*.

TABLE III. Distribution and degree of infection in Yellowtail.

Location	Depth	Date	Total No. fish examined	Percentage infection			
				None	Few	Numerous	Heavy
	fathoms						
St. Mary Bay	13	May, 1950	22	7	13	20	60
Chedabucto Bay	12–20	June 20, 1951	50	8	42	28	16
Bras d'Or Lakes	10–15	June 27, 1951	108	77	12	9	2
Banquereau		July 4, 1951	100	94	6	0	0

TABLE IV. Distribution and degree of infection in Winter Flounders

Location	Depth	Date	Total No. fish examined	Percentage infection			
				None	Few	Numerous	Heavy
	fathoms						
Gulf of St. Lawrence							
Shippegan, N.B.	Shoal	July, 1951	35	100	0	0	0
Nova Scotia inshore							
Bras d'Or Lakes, N.S.	3–10	July, 1950	53	97	3	0	0
Bras d'Or Lakes, N.S.	3–10	June, 1951	573	99	1	0	0
Chedabucto Bay, N.S.	10–20	June, 1951	100	27	40	23	10
Pubnico, N.S.	3–6	May, 1950	97	41	48	8	2
Bay of Fundy area							
Chignecto Bay, N.S.	8–10	June, 1951	50	100	0	0	0
Minas Basin, N.S.	10–20	July, 1950	45	98	0	0	2
Minas Basin, N.S.	10–20	July, 1951	366	93	4	2	1
Annapolis Basin, N.S.	10–20	July, 1951	383	23	46	27	4
Passamaquoddy Bay area, N.B.							
Oak Bay	5–8	Summer 1950	200	48	35	12	5
Oak Bay	5–8	Summer 1951	237	29	53	17	1
Passamaquoddy Bay	3–27	Summer 1950	792	23	23	13	41
Passamaquoddy Bay	3–27	Summer 1951	3,054	9	34	43	14
St. Mary Bay, N.S.	6–13	May, 1950	400	21	32	16	31
St. Mary Bay, N.S.	6	May, 1951	200	28	32	36	4
Gulf of Maine							
Small Point, Me.	unknown	June, 1951	33	58	21	21	0
Boothbay Harbour, Me.	unknown	June, 1951	33	6	37	57	0
Nantucket Point, Mass.	unknown	July, 1951	35	100	0	0	0

Yellowtail. *Limanda ferruginea* (Storer) (Table III)

DISTRIBUTION: Northern Gulf of St. Lawrence to New Jersey. Sandy bottom, rarely below 35 fathoms offshore and 20 fathoms inshore; on Nova Scotia offshore banks. Important commercially. Average commercial size 16 inches but may reach 22 inches.

SAMPLING DEPTHS: 10 to 20 fathoms.

INFECTION: Heavier inshore than offshore.

INFECTION CHARACTERISTICS: Cysts usually in the pterygiophoral muscles, but also occur along the fin membrane in "heavy" infections. Two "numerous" infections found in Passamaquoddy Bay in 1951. Johnstone (1905) reports a closely related species of fish heavily infected in the North Sea and off the coast of Scotland.

Brill or Windowpane. *Lophopsetta aquosa* (Mitchill)

DISTRIBUTION: Southern Gulf of St. Lawrence and New England to South Carolina. Sandy bottom; warm waters down to 15 fathoms. No commercial value. The smooth-skinned brill is scarce in Passamaquoddy Bay: 37 brill were collected as compared to 2,500 winter flounders.

SAMPLING DEPTHS: In Passamaquoddy Bay only at 5 to 20 fathoms.

INFECTION: Four infected fish out of 37 specimens collected in Passamaquoddy Bay. No brill reported infected with *S. baccatum* from the Massachusetts coast according to Moore (1947, p. 63). Infected fish were above 25 cm. in length.

INFECTION CHARACTERISTICS: Cysts, when present, scattered in muscles, never found in fin rays. Maximum observed infection—16 cysts in one specimen.

Smooth Flounder. *Liopsetta putnami* (Gill)

DISTRIBUTION: Ungava Bay to Providence, R.I. A brackish estuarine shoal water species, found on soft mud bottom down to 10 fathoms. Of little commercial importance.

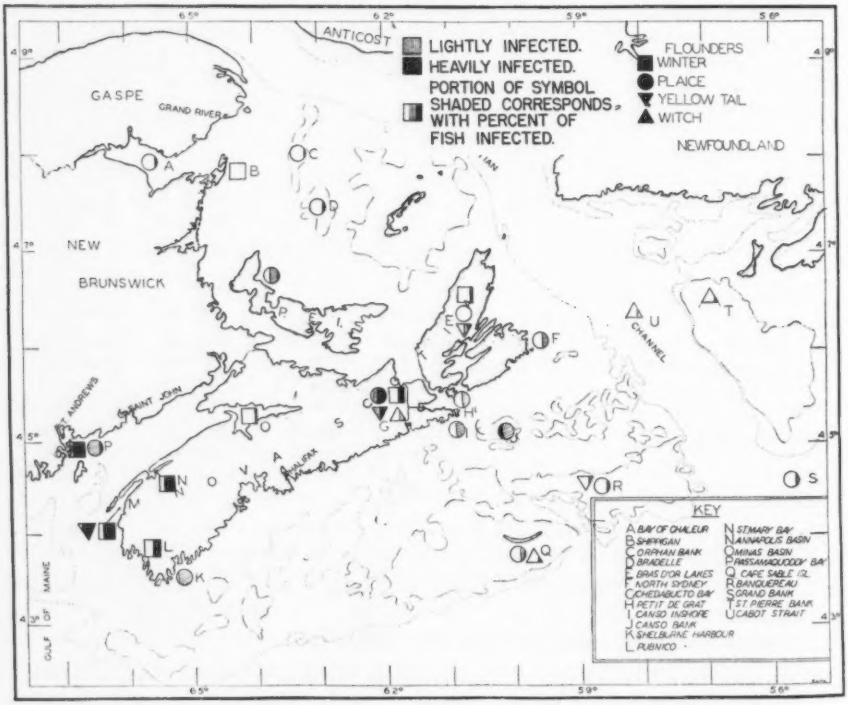

FIGURE 1. Distribution and degree of infection in eastern Canadian flounders.

SAMPLING DEPTHS: Intertidal zone and in brackish water. In Passamaquoddy Bay, down to 3 fathoms.

INFECTION: Fifty specimens examined—one specimen with two cysts, eight with one cyst each.

INFECTION CHARACTERISTICS: Cysts usually found at base of fin rays. One specimen had cysts in peripheral muscles.

Winter Flounder. *Pseudopleuronectes americanus* (Walbaum) (Table IV)

DISTRIBUTION: Labrador to Georgia, on mud, sand and clay bottom, common in depths down to 20 fathoms. Abundant inshore. Rarely larger than 18 inches and three pounds.

SAMPLING DEPTHS: Intertidal to 30 fathoms.

INFECTION: Heavier in deep than shoal water.

INFECTION CHARACTERISTICS: Smaller fish less heavily infected than larger specimens. Cysts may be found anywhere on ventral surface. Muscles are often heavily infected, as are fin membranes, dermal surfaces and subdermal tissue. Fish as small as 3.5 cm. have been found infected.

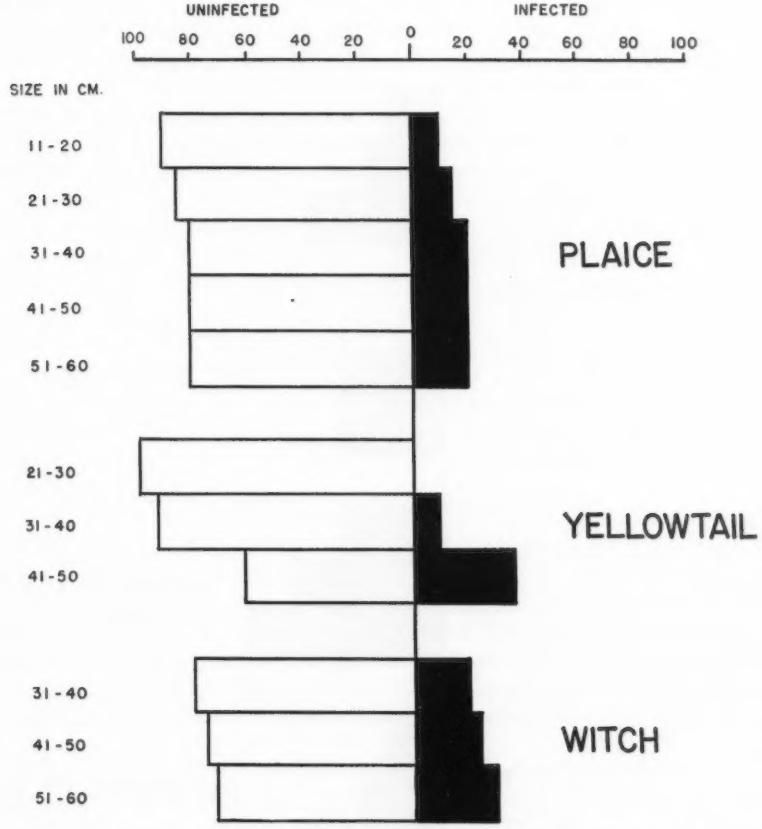

FIGURE 2. Size of plaice, yellowtail and witch flounder (offshore species) related to infection.

The observations on distribution and degree of infection in flounders are summarized in Figure 1. The heavily infected areas are in the lower Bay of Fundy and along the eastern shore of Nova Scotia and Newfoundland. There are practically no worms in plaice populations along the northern shore of New Brunswick and the south shore of Quebec. Only three of the 200 Orphan Bank plaice examined were infected and these with only one cyst each. On most offshore banks the incidence of S. *baccatum* is slightly higher.

SIZE AND INFECTION

The larger fish of each of the commercial species are more heavily infected than smaller fish (Fig. 2, 3). Among offshore species, both the yellowtail and witch flounder show a progressive increase in infection with increased size (Fig. 2). The plaice shows an increase up to 31 cm., but not beyond. The winter

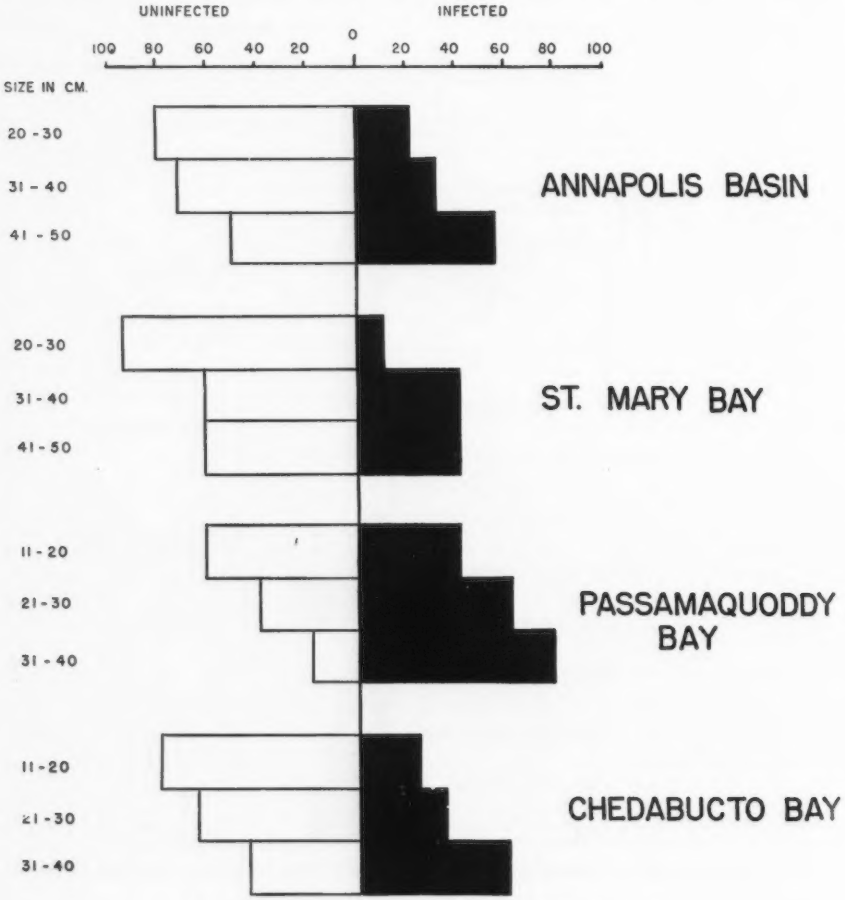

FIGURE 3. Size of winter flounder related to infection.

flounder (Fig. 3) was more heavily infected than other flounders in all of the areas examined, but shows the same increase of infection with size. Samples of both the brill and smooth flounders were so small, and these fish are so infrequently infected, that no relationship of size to infection was apparent.

DISCUSSION

Of all Canadian flatfish, the winter flounder is most frequently and heavily infected with metacercarial cysts of *S. baccatum*. It grows to its largest size and is most plentiful in the Bay of Fundy, in the southernmost part of which this flounder harbours the heaviest metacercarial infections of this parasite in Canada. The American plaice, witch and yellowtail are more common offshore, although some bays (e.g. Chedabucto Bay) of northern Nova Scotia do support large populations of plaice and witch which may be heavily infected with *S. baccatum*. On offshore grounds (where these species are especially abundant and fished commercially) their infection with the metacercaria is negligible, being limited to the occasional fish per sample containing a few cysts. Inshore and offshore flatfish of the northern Gulf of St. Lawrence are seldom infected and then with only one or two cysts per fish.

There is an indication that host specificity may be important in the infection of flatfish with *S. baccatum*. In Chedabucto Bay, where all commercial species are found, the winter flounder, yellowtail and plaice bear heavy infections; the witch, although frequently infected, is so to a low degree (only 2% "heavy" infection). Although the witch has often been taken along with other heavily infected flounders, it has not been found to be heavily infected.

The intensity of the infection of flatfish by *S. baccatum* is not solely related to the abundance of flatfish in an area. Minas Basin and the Bras d'Or Lakes have large numbers of winter flounders, and the former supports a commercial fishery, but both areas are almost free from *S. baccatum*. The American plaice is fished commercially in the northern Gulf of St. Lawrence, Baie des Chaleurs, and on the Grand Banks where infection incidence is negligible. However, when this species is taken in Passamaquoddy Bay (where it is not abundant) it is almost always heavily infected.

The life cycle of *S. baccatum* is completed by the transfer of infective stages from host to host, either by ingestion of the intermediate larval stage found in the flounder by a suitable carnivorous host in which the adult develops, or by passage of a free-living stage from a gastropod into the skin of the flounder. Therefore, unless the snail and carnivorous final host populations are large, the *S. baccatum* infection in the flounders in that area will be light or negligible. In the southern Bay of Fundy, a heavy inshore population of winter flounders represents a favourable situation for the efficient completion of the life cycle of this parasite.

S. baccatum was originally described from Europe for an adult trematode found in the halibut. Johnstone (1905) reported heavy infections of metacercarial forms which are recognizable as this species in *Limanda* (*Pleuronectes*) *limanda* in shoal waters off the coast of England. In Britain Nicoll (1915), Nicoll and Small (1909) and Lebour (1908, 1911) have reported metacercariae of *S.*

baccatum, and Dawes (1947) records as hosts six species of European flatfish. Most important to the present study are the witch and the long rough dab (American plaice), whose range and function as vectors of *S. baccatum* extend across the North Atlantic from Europe to our own shores.

A sample of long rough dab received from Norway's Norske Fjord in inshore waters was heavily infected with *S. baccatum* cysts, and other European studies of this fish suggest that it is lightly infected offshore. Thus there is good evidence for believing that the characteristics of the metacercarial infection in European flounders are similar to those of comparable Canadian hosts.

SUMMARY

1. All six pleuronectids of eastern Canada are infected with metacercarial cysts of *Stephanostomum baccatum*, an acanthocolpid trematode.

2. The areas of heaviest infection are the inshore waters of the lower Bay of Fundy.

3. The winter flounder is the most frequently and heavily infected flatfish, but plaice and yellowtail when taken in inshore waters may also be heavily infected. The witch, smooth and windowpane flounders are seldom heavily infected.

4. *S. baccatum* occurs in both the European and North American Atlantic. Records and specimens from European waters indicate that flatfish there may be more heavily infected in inshore waters than offshore as is the case in Canada.

5. Larger fish of these six species are more heavily infected than smaller ones.

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Studies of the Trematode *Stephanostomum baccatum* (Nicoll, 1907): II. Biology, with Special Reference to the Stages Affecting the Winter Flounder[1]

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ABSTRACT

Stephanostomum baccatum, an acanthocolpid trematode, has the following host succession in eastern Canadian waters: *Buccinum undatum* and *Neptunea decemcostatum* (Gastropoda), primary intermediate hosts; the six common species of pleuronenctids, second intermediate hosts; *Hemitripterus americanus* and *Hippoglossus hippoglossus*, common definitive hosts. Infection of flatfish is by penetration of the integument of the host by an atypical Ophthalmoxiphidiocercous cercaria.

The infection of the winter flounder, *Pseudopleuronectes americanus*, as investigated in Passamaquoddy Bay, N.B., shows the following characteristics:

1. The infection in inshore waters is greater near open water than on shoal grounds.
2. For any given location deeper water samples show a higher incidence of infection than shoal samples.
3. Larger fish have heavier infections than small ones.
4. The growth of the flounder is not impeded by heavy cyst infections.
5. No marked seasonal variation of infection can be demonstrated. Control is impractical.

INTRODUCTION

The flatfish of the Canadian maritime provinces are frequently and sometimes heavily, infected with the metacercarial cysts of *Stephanostomum baccatum* (Nicoll, 1907), an acanthocolpid trematode (Wolfgang, 1954) (Fig. 1). Studies of the life history and natural history of this worm were begun in the summer of 1950 and were continued during the summers of 1951 and 1952. Most of the experimental work was done at the Atlantic Biological Station, St. Andrews, N.B., though research was continued at the Institute of Parasitology, McGill University, Macdonald College, Que., during the winter months.

Stafford (1904) reported *S. histrix* in the winter flounder, *Pseudopleuronectes americanus* (Walbaum), caught in Passamaquoddy Bay. Huntsman (1902) reported finding small white cysts which from their description and location were almost certainly metacercariae of *S. baccatum* in the muscles of American plaice, *Hippoglossoides platessoides* (Fabricius).

In Europe, the same species of trematode occurs encysted in flatfishes of several species. Johnstone (1905) reported what is a *Stephanostomum* species from the flesh of *Pleuronectes limanda* (L.). Lebour (1907) reported *S. baccatum* from *Limanda limanda* (L.), from *Hippoglossoides platessoides* and from *Glyp-*

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tocephalus cynoglossus (L.). Nicoll and Small (1909) reported finding it in *Pleuronectes limanda* and at that time stated: "It is not at all improbable that the cercariae of S. *caducus*, S. *triglae* and S. *baccatum* are all to be found encysted in young pleuronectid fishes." Nicoll (1910) reported finding cysts of S. *baccatum* in *Hippoglossoides platessoides*. Examinations by the writer of specimens of S. *baccatum* encysted in flatfish from Norway and England indicate that probably all *Stephanostomum* cercariae in the flesh and fins of pleuronectids of the North Atlantic are S. *baccatum*, considering both the wide geographical range of the parasite, and the distribution of its intermediate and definitive hosts.

Records of adult *Stephanostomum* from Canadian Atlantic waters are confined to reports by Stafford (1904) for S. *sobrinum* in the sea raven, *Hemitripterus americanus* (Gmelin), from Passamaquoddy Bay; in the wrymouth, *Cryptocanthodes maculatus* (Storer) from Malpeque, P.E.I.; and in the Arctic eelpout, *Lycodes reticulatus* (Rheinhardt) at Canso, N.S. Manter (1926) found S. *baccatum* in the rectum of the halibut, *Hippoglossus hippoglossus* (L.), off Mt. Desert Island, Maine.

FIGURE 1. Cysts of S. *baccatum* in the fins and muscles of the winter flounder.

The genus *Stephanostomum* Looss, 1899, belongs to the trematode family Acanthocolpidae Lühe, 1909. Members of this family mature in marine teleosts; species of the genus *Stephanostomum* occur in marine fishes in all hemispheres. Manter and Van Cleave (1951) include 28 species and Caballero (1952) 30 species in the genus. However, the status of many species is in dispute owing to descriptions based on a small number of specimens and to the incomplete knowledge of morphological variation within individual species of the genus.

Stephanostomum tenue (Linton, 1898) is the only species of the genus whose life cycle was known until the present. Martin (1939) completed the life

cycle of this species at Woods Hole, Massachusetts, and found the primary intermediate hosts to be the snail, *Nassa obsoleta* Say, in whose digestive gland were found rediae and from which were liberated free-swimming, photopositive, ophthalmoxiphidia cercariae with a flame cell pattern of 2(3+3+3+3+3+3+3). The silverside, *Menidia m. notata* (Mitchill), the second intermediate host, became infected by ingesting these cercariae which are attached by their tails to its food. They subsequently encysted in its liver. The worm matured most commonly in the striped bass, *Roccus lineatus* Bloch, but was found in a number of carnivorous hosts, including the sea raven.

THE DEFINITIVE HOST OF *S. BACCATUM*

In the spring of 1950 examination of predatory fish for the presence of adult *Stephanostomum* was carried out in St. Mary Bay, N.S. No adults were found at this time, but numerous small cysts were recovered from the intestine of the sea raven, corresponding closely to the metacercarial cysts found in the winter flounders. Later examinations of the same species in Passamaquoddy Bay showed at least 30 per cent of the sea raven recta to be infected with *Stephanostomum* adults, later identified as *S. baccatum*.

The distribution of infected sea ravens, the most common inshore host, is wider than that of any one of the second intermediate hosts. It has been found infected at all depths from intertidal to below 120 fathoms and is collected in samples along with witch (*Glyptocephalus cynoglossus*), American plaice, and yellowtail (*Limanda ferruginea*), as well as with the inshore winter flounder.

Experimental proof of the relationship between the *S. baccatum* adults in the sea raven and the larvae in winter flounders was established in the summer of 1950 in the following manner. Holding pens were set up for three species: the sea raven; the long-horned sculpin, *Myoxocephalus octodecimspinosus* (Mitchill); and the common eelpout, *Macrozoarces americanus* (Bloch and Schneider). Three methods were used to induce infections.

1. Infected flounder flesh was presented to the fish.
2. Cysts dissected from the fins and muscles were forced under pressure into the fish's stomach from a bulb pipette while the fish was under anaesthetic (1 per cent urethane).
3. Gelatin capsules were filled with cysts taken from fins and muscles of the winter flounder and placed in the siphons of clams which were then fed to the fish.

Nearly all test fish and especially the common eelpout ate the siphons readily and with little or no regurgitation. The first two methods were discarded as unsatisfactory but the last proved simple and effective. Although several hundred cysts were used for each dose, no comparison between numbers of cysts introduced into experimental hosts and numbers of adult worms recovered could be made because their viability may have been impaired by dissection.

During this survey, infected sea ravens were taken from Passamaquoddy Bay, N.B.; Annapolis Basin, N.S.; St. Mary Bay, N.S.; Pubnico, N.S.; Shelburne, N.S.; Halifax Harbour, N.S.; Chedabucto Bay, N.S.; Bras d'Or Lakes, N.S.; Northumberland Strait, P.E.I.; the east coast of Labrador; Grand Manan, Bliss Island and Lepreau in the Bay of Fundy (Fig. 3, Wolfgang, 1954).

Examinations of other predatory fish (30 species of 953 individuals) in maritime waters showed one specimen of *S. baccatum* in the rectum of a short-horned sculpin, *Myoxocephalus scorpius* L., from Passamaquoddy Bay and one specimen in a halibut from LaHave Bank.

Table I lists the species used in experimentation together with the success of infection tests; only positive results are presented.

TABLE I. Results of the experimental infection with *S. baccatum* of sculpins, eelpout and sea ravens.

Pen No.	Host	Time lapse between feeding and examination	Number of adult worms recovered
		days	
1	sea raven	7	9
2	sea raven	4	123
3	eelpout	9	20
4	sea raven	10	98
5	sea raven	10	15
6	eelpout	19	11
7	eelpout	17–15[a]	86
8	sculpin	15	3
9	eelpout	22	1

[a]100 cysts were given on each of three successive days.

The common eelpout is the most important test animal in the series because it is not found infected in nature, probably because it feeds mainly on molluscs and echinoderms and seldom eats fish. Infection in sea ravens due to experimental feeding of cysts was easily differentiated from natural infection, because naturally acquired worms were larger and sexually mature, whereas worms from experimental infections lack well developed vitellaria and were small.

Further evidence that the sea raven serves as an efficient definitive host was obtained during the winter of 1950–51 when several sea ravens and numerous flounders of all sizes, which were to be used for behaviour tests, were held in the same tank. The sea ravens ate most of the smaller flounders, and on examination of the recta of the sea ravens two specimens were each found to contain over 2,000 small but firmly attached *Stephanostomum baccatum*. As the greatest *natural* infection was 567 almost-mature worms from a sea raven taken near Clam Cove Head, Deer Island, N.B., these results strongly suggest that the infection was acquired during the period in the tank.

FIRST INTERMEDIATE HOST OF *S. BACCATUM*

In June 1952, in the St. Croix River, the marine gastropods, *Buccinum undatum* L. and *Neptunea decemcostatum* Say, were found to be infected with eyed cercariae measuring about 1 mm. from oral sucker to tip of tail. A total of 13 infected snails have been recovered thus far from depths ranging from the

sub-littoral zone to 40 fathoms. Deep-water specimens were dredged with a fine-mesh scallop drag.

In heavily infected gastropods the gonads and digestive glands are packed with larval stages of *S. baccatum*. Only rediae containing cercariae were recovered from such specimens whereas rediae containing germ balls and what looked like daughter rediae were taken from one relatively lightly infected snail. The presence of the larvae could not be detected by external observation of molluscs since most of the infected *Buccinum* are large, and retaining them in sea water in finger bowls was never satisfactory. Positive infection of *Buccinum* and *Neptunea* was ascertained only by dissection. The incidence of infection in *Buccinum* was about 1 per cent of 875 specimens, with indications that infection was higher offshore. *Neptunea* was infected in 6 per cent of 125 specimens. Infected snails have been recovered from: Lepreau Ledges, Grand Manan (Bay of Fundy) and inside Passamaquoddy Bay from Joe's Point, Clam Cove Head, Pendleton-Deer Islands and Brandy Cove.

The cercariae of *S. baccatum* have two eyespots, a long prepharynx and a pronounced set of cephalic cystogenous glands. There is, however, no oral spine as in the cercaria of *S. tenue*. Study of the flame cell pattern is difficult and although several hundred cercariae were examined, no complete count of these cells could be made. When the cercaria begins to die, the main lateral excretory tubules enlarge so that they obscure all side branches of the excretory system. There is a spatulate tail of about the same length as the body of the cercaria, which may assume various shapes in contraction. The body proper is filled with vacuoles and opaque masses.

The natural method of cercarial release was not observed but it is probably by rupture of the mantle membrane. The cercariae when dissected out are quite active; they swim tail foremost for only a few seconds, then settle, beating the tail violently back and forth with the body curled up in a ball. Once settled they attach by the tail and begin exploratory creeping in all directions. The tail is easily lost, and cercariae may be found in the bottom of the watch glass, crawling slowly by means of their suckers. In the presence of strong sunlight or artificial light, they react by moving violently, thrashing their tails and contorting their bodies, but settling down to a slow crawl when the light is removed. The tail is independently motile and may beat spasmodically for several hours after it is lost from the body.

Cercariae are released from the rediae into the gonad and digestive gland of the snail and both rediae and cercariae feed actively on gland cells. These larvae seem to castrate the snail as there are no sperm or ova produced in the gonads and the proliferation of larvae within the digestive gland is extensive. There is no indication that the snails are killed by the infection but whether they ever completely recover was not learned. The life span of the cercaria once removed from the host is not known, but in unchanged sea water the cercariae lived for 72 hours. Unless removed from the snail, they died soon after its death.

In all dissected snails most of the mature cercariae lay along the mantle membrane, whereas most immature cercariae and rediae were found deeper in

the gonad and digestive gland. This location of cercariae suggests a peripheral migration of larval forms from the region of the gland around the intestine to the centre of the gland masses and finally to the periphery.

SECOND INTERMEDIATE HOST OF *S. BACCATUM*

Preliminary experimental infections of winter flounders with *S. baccatum* were conducted in glass trays filled with sea water containing several hundred cercariae dissected from infected snails. These tests showed clear evidence of external penetration and newly encysted and encysting cercariae were easily differentiated from naturally acquired cysts.

Because of the size of these cysts, more conclusive evidence of the mode of infection was obtained by using small winter flounders from 2.5 to 5.0 cm. long. These small fish were fragile and transparent so that under a dissecting microscope any previous infection could be detected and used as a check against artificial infection. Each small flounder was exposed to several thousand cercariae dissected from the digestive glands of three specimens of *B. undatum*. Since cercariae in all stages of development occur in the glandular tissue of the snail, no estimate of the number of cercariae capable of penetrating the skin of the winter flounder can be made. The results of this experiment are tabulated in Table II.

TABLE II. Experimental infection of winter flounders by cercariae of *S. baccatum*.

Size of flounder	Previous cysts	Duration of exposure	Number of penetrated cercariae
cm.		*minutes*	
2.5	0	10	2
2.5	0	10	1
3.5	1	15	2
4.0	2	10	4
4.5	1	10	5
4.6	2	10	3
5.0	2	15	10

The cercariae do not swim toward the flounder but wait until they are touched by the fish. The cercaria then grasps the flounder by means of one of its suckers or by its prehensile tail and begins to wander short distances (1 cm. each way) over the surface of the fish. Those finding suitable sites for entry begin burrowing, using the extremely motile anterior region of their body.

The delicate body structure of small flounders and their low resistance to adverse conditions makes handling of these small fish difficult and under experimental conditions they live for under two days. In most cases such experimentally infected fish showed penetrated cercariae to be still free in their musculature.

The experimental evidence for external penetration is supported by the following characteristics of natural *S. baccatum* infections in winter flounders.

1. Younger and more immature cysts are always found along the external surfaces of the flounder whereas well-developed cysts are deeper.
2. The infection is asymmetrical: cysts occur more frequently on the ventral than on the dorsal surface. It is the ventral surface which is in intimate contact with the bottom and consequently is more exposed to physical contact with the cercaria.
3. Flounders of very small size (3.5 cm.) are infected only on the ventral surface; until flounders are large enough to cover their fins and dorsal surfaces with bottom debris, they are not infected at all along the dorsal surface or in the fin membrane.
4. In the cottid fish which serve as facultative hosts, cysts occur in the gills, whose rakers and gill-arch teeth often contain mud from their grovelling.
5. No cysts of *S. baccatum* were found in any visceral organs or inside the pleural cavity.

The infection of pleuronectid fish varies slightly in its manifestations from species to species. In the winter flounder subcutaneous cysts are most commonly found near the pterygiophoral septum separating the lateral interspinose muscles (or pterygiophoral muscles) from the myotomes. There is always a deposit of globular fat at the base of these muscles through which cercariae do not seem to penetrate. In "heavy" infections, dermal cysts are found all over the ventral peripheral surfaces and may in extreme cases give the fish a rough "measley" appearance. In heavily infected fish, 15–25 cm. long, the fins also become filled with cysts. This may be due to direct penetration of the fin membrane and encystment, or due to blockage of the path of entry of the cercaria at the base of the fin ray into the muscles. When the channel behind the fin rays is obstructed either by a previously encysted cercaria of *S. baccatum* or by some other trematode such as *Cryptocotyle lingua* (Creplin), the cysts tend to pile up one behind or beside the other in the available space. It was often noted that cysts in fins of heavily infected fish were not as large as cysts in light infections; this size difference may have been a result of crowding.

The cercaria encysts in muscles or connective tissue by secreting about itself a hyaline cyst within which it moves and grows. This newly encysted metacercaria, which is about 0.4 mm. long, increases in length to 2.4 mm. During this growth period the metacercaria coils upon itself inside the cyst, gonads develop and eyespots diminish in size. The host lays down a layer of opaque, white connective tissue around the transparent parasite shell. This white layer is commenced immediately after encystment but is not usually thick enough until the second year to render the characteristic white fibrous cyst visible to the naked eye.

There was never, in all the cysts dissected, any indication that the winter flounder kills the cercaria. A local irritation of host muscle was the only change seen on histological sectioning of the cyst. *C. lingua* which often occurs in winter flounders in Passamaquoddy Bay, unlike *S. baccatum*, enters the host by rapid penetration and may travel through the blood vessels to the encystment site. There is a pronounced host reaction to *C. lingua* in that black pigmented connective tissue is rapidly laid down by the host about the cyst. No difference

in the behaviour of infected as opposed to uninfected flatfish could be demonstrated.

THE EGG

Two types of eggs are commonly found in *S. baccatum* adults. In stained and mounted specimens one is ribbed and transparent; the other is oval, smooth and contains an embryo. Both eggs measure 75 to 90μ. The ribbed egg is common during the spring and summer and is replaced by the smooth egg in the late autumn and winter. Attempts to hatch these eggs have been confined to the ribbed egg since that was the form available when the investigation was being conducted. In none of the tests did the eggs hatch nor did they produce rediae when fed to the known primary intermediate hosts. It is assumed that they are either infertile or nonviable eggs and that the smooth-shelled, oval, fertile eggs are produced mainly in the colder months of the year.

BIONOMICS OF THE METACERCARIAL STAGE IN THE WINTER FLOUNDER

The winter flounder is the logical host on which to base a study of the habits of the metacercaria. Movement and distribution of the other vectors of *S. baccatum* are neither well known nor readily available; location of snail populations in the Bay is also poorly known and sea raven movement cannot be predicted. Furthermore, the adult worm is only a temporary inhabitant in their recta and the infection is too variable to serve as a basis for conclusions. The winter flounder as the second intermediate host bears its infection for life, accumulating a larger number of parasitic cysts as it grows older and larger. This fish, which is always available in large numbers, is believed to have a relatively restricted movement. Until recently it has been an unexploited species, being sought only for lobster bait and occasionally as food for local inhabitants. In 1949 a commercial fishery for the winter flounder as a commercial food product was established in inshore waters of the Bay of Fundy and subsequently in other inshore waters throughout the maritime provinces. Information from commercial landings was a valuable addition to local sampling in Passamaquoddy Bay. The results of investigations in Passamaquoddy and St. Mary Bays conducted in 1950 and 1951 to determine the relationship of metacercarial *S. baccatum* infection to the winter flounder are presented below.

Passamaquoddy Bay opens along the western coast of the Bay of Fundy. It is bordered on the south by Deer Island, Cobscook Bay and Maine, on the north and east by New Brunswick, and on the west by Maine. It is a shallow bay ranging in depth down to 30 fathoms but with an average of about 15 fathoms. The bottom is generally muddy but areas of rock and sand are shown on charts near the main passages at Western and Letite Passages as well as at the mouths of the St. Croix River and the Magaguadavic River. Low salinity areas (28 per cent of normal sea water) occur in Oak Bay and the upper St. Croix River, where the Digdeguash and Magaguadavic Rivers have low salinity basins near their mouths. Circulation is from north to south through Letite Passage. The average tide range is about 24 feet with 21 feet at neaps and 27 at springs. These

characteristics of the Bay are important in considering it as an environment for *S. baccatum*, because the lower inshore waters of the Bay of Fundy represent the highest infection areas recorded for the parasite. The winter flounder is not exploited commercially here and is, therefore, relatively undisturbed.

Factors influencing parasitism of winter flounders which will be considered in the following discussion are location (geographical point of sampling), depth of sampling, size of host with relation to its infection, age (with an aim at checking growth rate against infection) and seasonal variation in infection.

Samples of winter flounders taken in both Passamaquoddy and St. Mary Bays were studied in the following way:

Individual flounders were measured and the dermal surfaces, including fins, examined for the presence of *S. baccatum* cysts. A slit was then made down the lateral line on the ventral surface from the visceral mass to the tail and the muscles on the ventral surface laid back to the backbone. The musculature was then examined for cysts. During the 1951 sampling in Passamaquoddy Bay only skins were examined, but otoliths were collected from a portion of each sample. In St. Mary Bay, where catches were frequently large, only random samples of the catch were examined.

For convenience in recording data, the degree of infection per fish was divided into four categories based on the ease with which cysts could be seen (see Fig. 2). They are:

"None"—no cysts plainly visible after close inspection of the surface.

"Few"—no cysts plainly visible at a glance but scattered cysts (usually under 10) discovered on close inspection.

"Numerous"—cysts plainly visible at a glance although not so massed as to obscure host body surfaces; cysts in this category were usually concentrated at the base of the fin rays but were also scattered in the fins.

"Heavy"—cysts crowded into the whole available surface area, the skin often being rough from cysts and the dorsal surfaces frequently with cysts in the pterygiophoral region.

1950 Investigations

A primary investigation of geographical location with reference to intensity of infection was carried out in 1950 in Passamaquoddy and St. Mary Bays.

PASSAMAQUODDY BAY. Sampling stations are listed with numbers which will serve to identify them on the map of Passamaquoddy Bay (Fig. 3).

1. Waweig River
2. Oak Bay
3. Brandy Cove
4. St. Andrews Harbour
5. Minister's Island
6. Bocabec Bay
7. Hardwood Island
8. Hydrographic Station 848
9. Pendleton-Deer Islands
10. Mascarene

The incidence is graded in decreasing order with relation to the distance of the sampling area from the open sea. As may be seen in both Tables III and IV and Figure 4, the categories "none" and "few" are closely related, and "numerous" and "heavy" are similarly related.

It will be noted that, for a given area, the infection in the fins is greater than the infection in the muscles. The correlation between the two infections, although

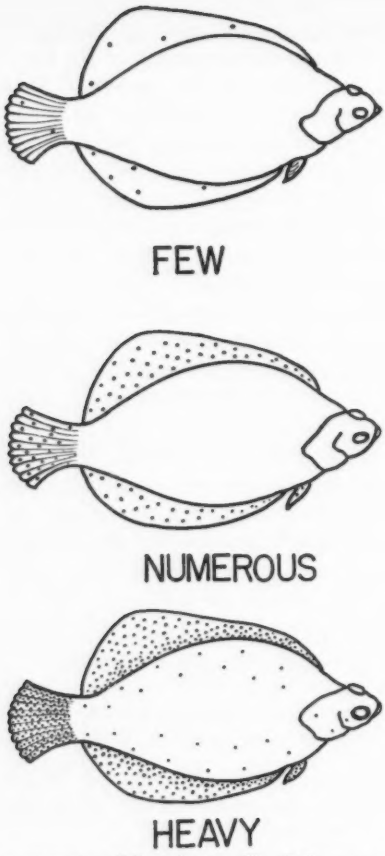

FIGURE 2. Three categories of fin infection "few", "numerous" and "heavy".

TABLE III. The incidence of cysts of *S. baccatum* in the fins of the winter flounder in Passamaquoddy Bay.

Locality	Date	Depth	Percentage incidence				Total fish
			None	Few	Numerous	Heavy	
		fathoms					
Waweig River	July	inter-tidal	63	30	5	2	92
Oak Bay	August	3–12	32	41	19	8	184
Brandy Cove	July	inter-tidal	59	22	5	14	83
St. Andrews Harbour	July	1–2	31	37	20	12	50
Minister's Island	July	3–16	9	31	10	50	116
Bocabec Bay	July	1–3	31	33	14	14	78
Hardwood Island	July	11–16	8	30	23	39	204
Station 848	June-July	22	28	15	5	52	54
Pendleton-Deer Islands	July-August	12–25	9	7	8	76	136
Mascarene	August	28–30	3	8	17	72	65

FIGURE 3. Passamaquoddy Bay flounder collection stations, 1950: 1. Waweig River; 2. Oak Bay; 3. Brandy Cove; 4. St. Andrews Harbour; 5. Minister's Island; 6. Bocabec Bay; 7. Hardwood Island; 8. Hydrographic Station 848; 9. Pendleton-Deer Island; 10. Mascarene.

TABLE IV. The incidence of cysts of *S. baccatum* in the muscles of the winter flounder in Passamaquoddy Bay.

Locality	Date	Depth	Percentage incidence				Total fish
			None	Few	Numerous	Heavy	
		fathoms					
Waweig River	July	inter-tidal	73	14	7	6	98
Oak Bay	August	3–12	47	37	8	8	184
Brandy Cove	July	inter-tidal	24	38	19	19	47
St. Andrews Harbour	July	1–2	49	33	9	9	45
Minister's Island	July	3–16	30	25	14	31	110
Bocabec Bay			No data available				
Hardwood Island	July	11–16	26	37	11	26	194
Station 848	June-July	22	23	26	30	21	43
Pendleton-Deer Islands	August	12–25	9	33	14	44	123
Mascarene	August	28–30	6	26	9	59	65

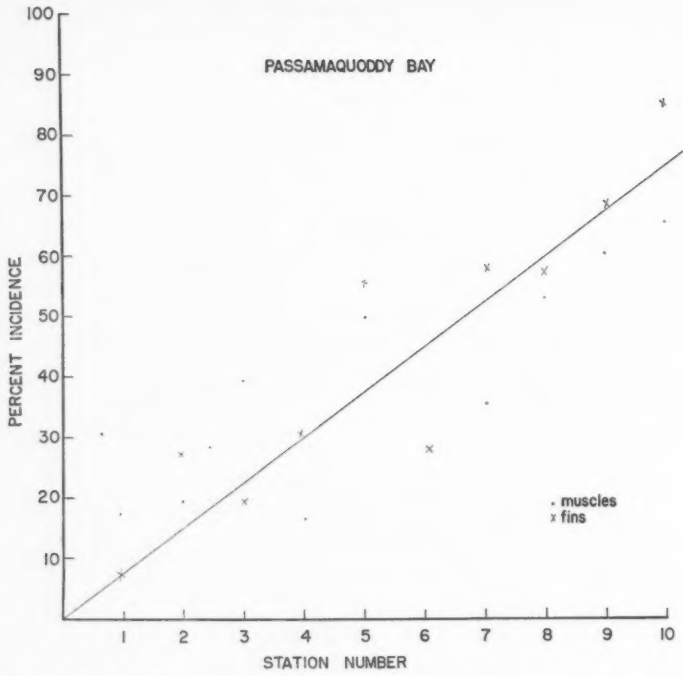

FIGURE 4. Percentage incidence of infection in relation to station numbers shown in Figure 3 for Passamaquoddy Bay.

not graded, shows the same general trend of increase from shoal to open water. Because of this, and also because muscle examinations are cumbersome, they were dropped in 1951.

ST. MARY BAY. Examination of winter flounders from St. Mary Bay, N.S., was carried on in conjunction with tagging experiments on the motor vessel *J. J. Cowie* during May, 1950 (Fig. 6). Flounder populations in St. Mary Bay are known to be distinct from those in Passamaquoddy Bay because of their more rapid growth rate. Table V gives infection data for St. Mary Bay.

TABLE V. The incidence of cysts of *S. baccatum* in the fins of the winter flounder in St. Mary Bay.

Locality	Date	Depth	Percentage incidence				Total fish
			None	Few	Numerous	Heavy	
		fathoms					
Gilbert's Cove	May	3–6	24	44	14	18	50
White's Cove	May	3–12	20	31	17	32	281
Church Point	May	9–12	18	30	15	37	124
Little River	May	13	20	24	20	36	50

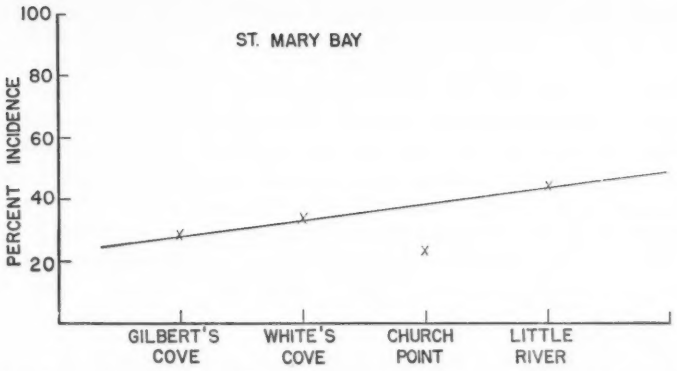

FIGURE 5. Percentage incidence of infection in relation to locations in St. Mary Bay shown in Figure 6.

FIGURE 6. St. Mary Bay flounder collection stations, 1950.

Figure 5 shows that the relationship of infection to location in St. Mary Bay is similar to that in Passamaquoddy Bay. However, in St. Mary Bay sampling was done in depths from 3 to 13 fathoms while in Passamaquoddy Bay the range was intertidal to 30 fathoms. Another important difference in the results of sampling in these two bays was the size range of fish: in St. Mary Bay no fish were taken less than 20 cm. long and the maximum size was over 40 cm.; in Passamaquoddy Bay no fish were taken over 40 cm. in length but fish as small as 10 cm. long were taken in drags. The difference in infection between Gilbert's Cove further north and Church Point, the farthest point south in the Bay, is only 19 per cent, but this distance is relatively short as can be seen in Figure 6. The tendency is for infection to increase toward open water.

1951 Investigation

In 1951, sampling in Passamaquoddy Bay was organized to show more closely the relationship of depth to infection intensity as well as relationships of size, age and seasonal collections to the degree of infection. Three main localities (called series I, II and III) were chosen for sampling to obtain data on local infection intensity. Each local had four sampling stations separated by five fathom depths (see Table VI).

The first locality chosen was the St. Croix River system—because it was the widest river and most variable salinity area in the bay. The second was near Minister's Island, because no large rivers or bay openings influenced it. The third was Oven Head. Station 12 lies inside and in line with Big Letite Passage.

Table VI. Sampling locations, arranged by series and depths.

Locality	Depth of station in fathoms			
	1–5	6–10	11–15	16–20
Series I	1	2	3	4
Series II	5	6	7	8
Series III	9	10	11	12

Samplings were made on a monthly basis from May through September. All stations were visited as close to the same time each month as possible but non-availability of station equipment and breakdowns made necessary some omissions and revisions. Station 1 in Oak Bay was sampled every month except June; Stations 2 and 3 were sampled in May, July and September; Station 4 never yielded a sufficient number of flounders on which to base a conclusion concerning its infection incidence. Series II and III Stations were visited each month and represent the largest source of data. Table VII summarizes the results of this sampling.

In the locality summations, the infection incidence follows the same general pattern as for 1950. In a station-by-station review of the data it will be seen that Station 3 (an area not sampled in 1950) represents a high-infection area near the

TABLE VII. Incidence of *S. baccatum* cysts in the fins of winter flounders, May-September, 1951, Passamaquoddy Bay.

Series No.	Station No.	Percentage incidence				Total fish
		None	Few	Numerous	Heavy	
I	1	29	53	17	1	237
	2	4	28	49	19	57
	3	3	10	56	31	87
	4	Insufficient number of fish to make determination				
	Total for series	19	40	30	11	381
II	5	34	44	17	5	368
	6	14	37	39	10	404
	7	3	28	51	18	579
	8	1	22	53	24	298
	Total for series	12	33	40	15	1,649
III	9	12	39	39	10	247
	10	9	35	37	19	429
	11	6	26	48	20	226
	12	3	32	43	22	158
	Total for series	8	32	42	18	1,060

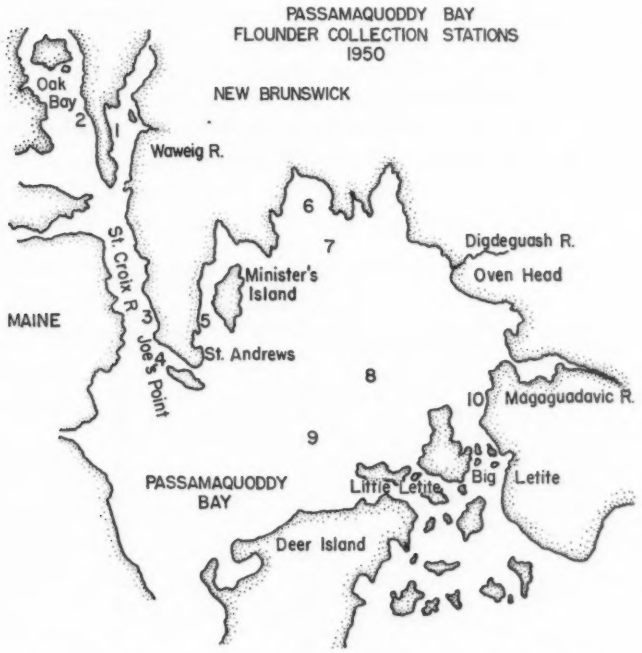

FIGURE 7. Passamaquoddy Bay flounder collection stations, 1951.

shore and at some distance from the mouth of the bay. It was this area which was sampled successfully for the presence of infected gastropods in 1952.

Figure 8 plots the data by infection categories and shows that the differences between high infections and low infections decrease for each location, regardless of depth, as the station distance from the mouth of the bay becomes less. This means that infection in flounders for any depth is approximately the same near Oven Head (Series III), but greatly variable at different depths in the St. Croix River from Oak Bay to Joe's Point (Series I). This trend toward a homogeneous population infection near the mouth of the bay (Fig. 9) seems to be related to the terrain of the shore, which is steep at Series III but has a gentle slope and long mud flats at Series I.

The high infection at Series III is definitely not associated with abundance of *P. americanus*, since the largest numbers of fish taken per area were in Series II and in Station 1 of Series I, which have lower infections.

Depth

Tables VIII and Figure 10 show the incidence of infection in relation to depth.

In each locality there is an increase in infection corresponding to an increase in depth, but this holds true only down to 11–15 fathoms. This difference of infection with depth is related in part to the size of fish, since larger fish, which are also the most heavily infected, occur most frequently in deeper water. However, small flounders, 9–15 cm. in length, when taken in deeper waters are frequently heavily infected, whereas they are usually lightly infected in shoal waters. Depth should be considered an important factor in infection only with respect to the general location where that depth occurs.

Table VIII. Incidence by depth of *S. baccatum* cysts in Passamaquoddy Bay.

Depth	Station	Percentage incidence	
		None or few	Numerous or heavy
fathoms			
1–5	1	82	18
	5	78	22
	9	51	49
6–10	2	32	68
	6	51	49
	10	44	56
11–15	3	13	87
	7	31	69
	11	32	68
16–20	8	23	77
	12	38	65

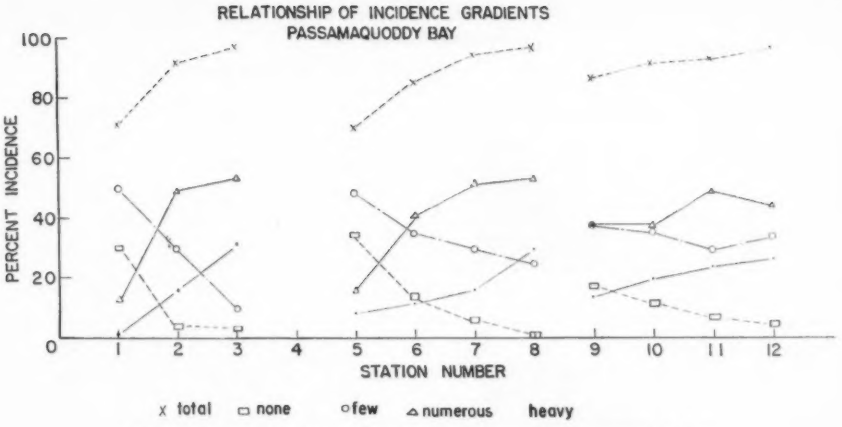

FIGURE 8. Relationship of incidence gradients, Passamaquoddy Bay.

SIZE OF FLOUNDER

The size factor is most important in getting a true picture of the infection in winter flounders. Small fish (below 9 cm.) taken during the summer, represent fish of that summer's spawning and date the earliest time at which a flounder may be infected. Flounders of the year seined in mid-summer onshore and taken in surface plankton tows near shore, are never found infected. However, the smallest metamorphosed flounders taken (3.5 cm. in length) were infected to a light degree at the end of August. Table IX gives an indication of the frequency of infection with regard to size in these small fish.

Figure 11 shows the relationship between the size of the flounder and the intensity of infection. In all locations larger flounders are more heavily infected than smaller fish.

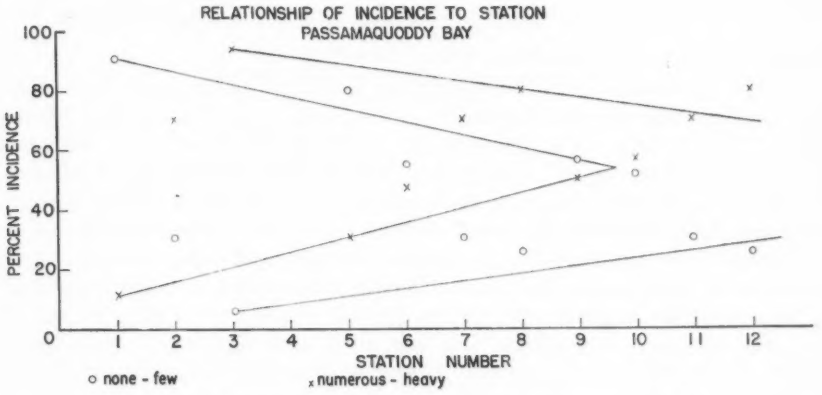

FIGURE 9. Relationship of incidence to station, Passamaquoddy Bay.

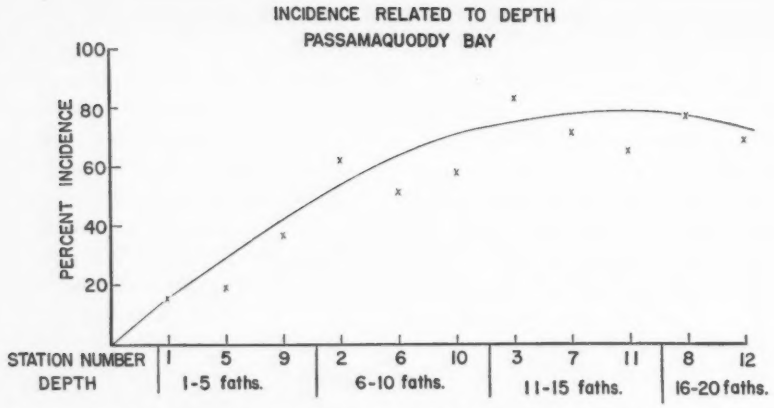

FIGURE 10. Percentage incidence of infection in relation to depth, Passamaquoddy Bay.

TABLE IX. Size frequency of fish and degree of infection with cysts in small winter flounders signed during August and September near Joe's Point in the St. Croix River.

Number of cysts	Size of fish in centimeters											
	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0
0	5	6	13	4	18	15	9	5	3	3	2	2
1	1	2	2	3	3	5	4	2	4	2	1	...
2	...	...	...	...	1	5	2	1	2	2	1	...
3	...	...	...	...	4	1	2	...	1	...	2	...
4	...	...	2	1	...	1	...	1	...	...	...	...
5	...	...	...	1	1	...	...	...	1	...	...	...
6	...	...	...	...	...	...	1	2	...	...	...	...
7	...	...	...	...	...	1	1	...	...	1	...	...
8	...	...	...	...	1	...	...	...	...	...	...	...
9	...	...	...	1	1	...	2	...	...	...	...	...
10 or more	...	...	...	...	2	2	1	2	...	1	...	...

DEGREE OF INFECTION RELATED TO AGE OF FLOUNDER

Since the number of cysts in the winter flounder is related to the size of the fish, it follows that the infection may be related to the growth of the host. During the summer of 1951, about 1,500 otoliths were collected from winter flounders in Passamaquoddy Bay and later read to determine the relationship of infection to age. These data were used to determine the effect of infection upon the rate of growth. Only those otoliths which could be read with certainty were recorded.

Table X is a summary of age-infection data grouped under heavy and light infections. It will be seen that sizes of heavily infected fish are nearly the same as those of lightly infected or uninfected fish. Infected fish are slightly larger, but this size difference is considered unimportant in view of the wide variation in length of fish within each age-group. Therefore, it can be safely stated that there is little if any effect on the growth rate of the flounder by parasitism with *S. baccatum*.

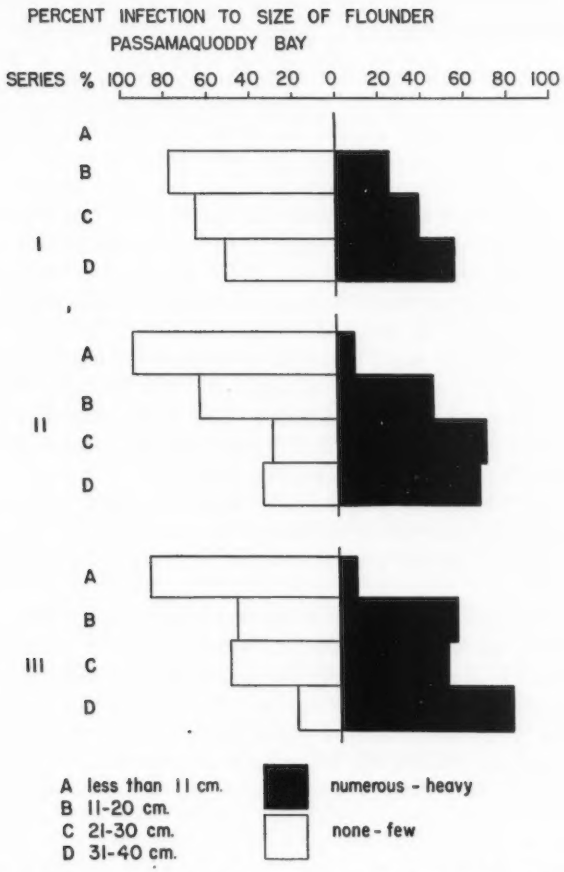

FIGURE 11. Percentage infected in relation to size of flounder, Passamaquoddy Bay.

TABLE X. The relationship between infection with cysts of *S. baccatum* and the size and age of winter flounder.

Age of fish	Uninfected and lightly infected fish		Heavily infected fish	
	Mean size	Total No.	Mean size	Total No.
	cm.		*cm.*	
1	14.5	8	18.0	20
2	19.0	31	20.0	40
3	20.9	37	22.8	56
4	23.8	91	24.8	78
5	25.8	202	26.3	155
6	27.8	181	29.7	125
7	30.0	76	30.6	41
8	31.0	40	31.9	20

Seasonal Variation of Infection

Collecting of samples in Passamaquoddy Bay began about mid-May and ended the first of October 1951. An attempt was made to sample at approximately the same time each month. Figure 12 shows the seasonal character of the heavier infection categories based on the percentage of heavy and numerous infections per sample plotted month-by-month for each station. Series I is omitted from this section because collections in the St. Croix River were erratic and incomplete except for Station 1, which is included with Stations 5, 6, 7 and 8.

The shoal water stations, 1, 5 and 9, show an increase in infection during the summer followed by a sharp decline in September. This drop is due to the entrance into the catches of small, relatively uninfected flounders. The stations at which marked changes could be noted were those located at depths between 5 and 15 fathoms. It is within this depth range that flounders first appear to become heavily infected. Commercial-sized flounders do not show much variation in infection in Passamaquoddy Bay. By the time they reach 25 cm. in length they are generally infected in the "numerous" category.

In Oak Bay (Station 1) larger fish seldom show heavy infections and no appreciable difference in the infection of commercial-sized fish was noted, although the infection for the area as a whole reached a high of 30 per cent in August.

It would seem that the infection of winter flounders might take place at any time, since snails infected with *S. baccatum* were collected from June through September with little change in number of the snails or in degree of infection.

Small flounders (3.5 cm.) which represent the spawning of the year in which they were taken (1951) were infected. Since these fish were estimated to be about three months old when caught, the infection must have taken place near the end of July. Small cysts are constantly appearing in the fins of flounders all summer

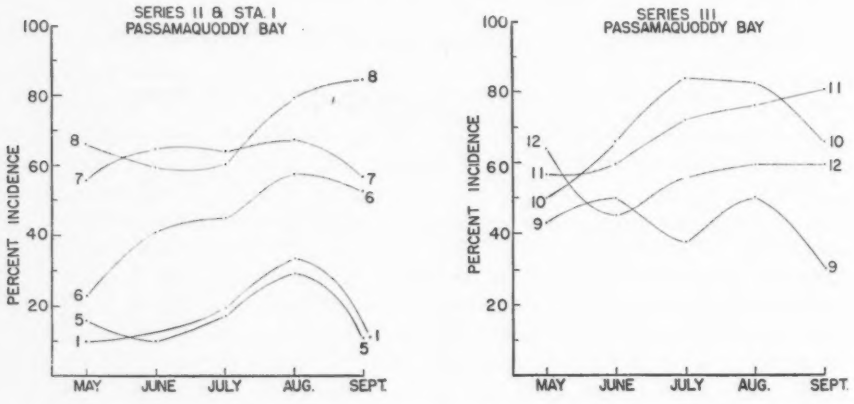

Figure 12. Seasonal variation in percentage incidence for Passamaquoddy Bay, 1951.

long and recently encysted cercariae have been demonstrated by dissection in the pterygiophoral muscles from April through October.

Seasonal increase in infection of winter flounders by S. *baccatum* as reported by St. Mary Bay fishermen was not substantiated by the present investigation.

DISCUSSION

The data presented show that flounders are infected most heavily when they live in deeper water and when they are large in size. There is no gross pathological effect due to parasitism; the infection throughout the summer months is continuous, not showing any marked variation in intensity, and the infection of flounders with S. *baccatum* varies from locality to locality.

Figure 13 is a pictorial representation of the life cycle of S. *baccatum* as it occurs in Passamaquoddy and St. Mary Bays. The sea raven at the top is the definitive host and has the adult worm in its rectum; the egg (down arrow) is presumably eaten by one of two species of gastropods; either *Buccinum undatum*, crawling on the rocks and behind the flounder on the bottom, or *Neptunea decemcostatum*, partially burrowed into the bottom and above the cercaria in the foreground. The cercariae emerging from both *Neptunea* and *Buccinum* (inset bottom centre) are free-living and crawl or adhere to the bottom particles. When they come in contact with a flounder, they penetrate the ventral dermal surfaces or, occasionally, the dorsal surfaces when the flounder throws bottom debris over itself (the dotted flounder represents this type). Encystment follows in the fins, skin or somatic muscles (inset above flounder in foreground). Completion of the life cycle involves eating of the flounder by the sea raven and the subsequent encysting and establishment of the larval worm in the rectum of the sea raven, where it grows to maturity and produces eggs.

Little has been published concerning any of the hosts: the best known host, however, is the winter flounder, the subject of the present study. Previously, Lobell (1939) and Perlmutter (1947) published data on the movements and biology of the fish in New York and New England waters. Perlmutter (1947), summarizing what is known for their biology, wrote:

> Considering the data as a whole, it appears that the blackback flounder (winter flounder) population is comprised of many independent, localized stocks inhabiting the estuaries along the coast. Any movement of fish away from these areas, other than seasonal, is not a directed migration but rather a gradual dispersion from population centres, a characteristic phenomenon with non-migratory animals.

Again, he states:

> 1. In any area the young of the blackback flounder are mostly the product of local spawning; 2. They remain in the shoal water near the shores of the bays and estuaries during the first year of life; 3. As they grow older they tend to move off into adjacent deeper water, and in the second and third years they begin entering into the catch of the commercial and sports fisheries.

The winter flounder in southern waters (New England and New York) shows a reversed habit from those in the Bay of Fundy in that it moves inshore and spawns during the winter, hence the name, winter flounder. In the Bay of

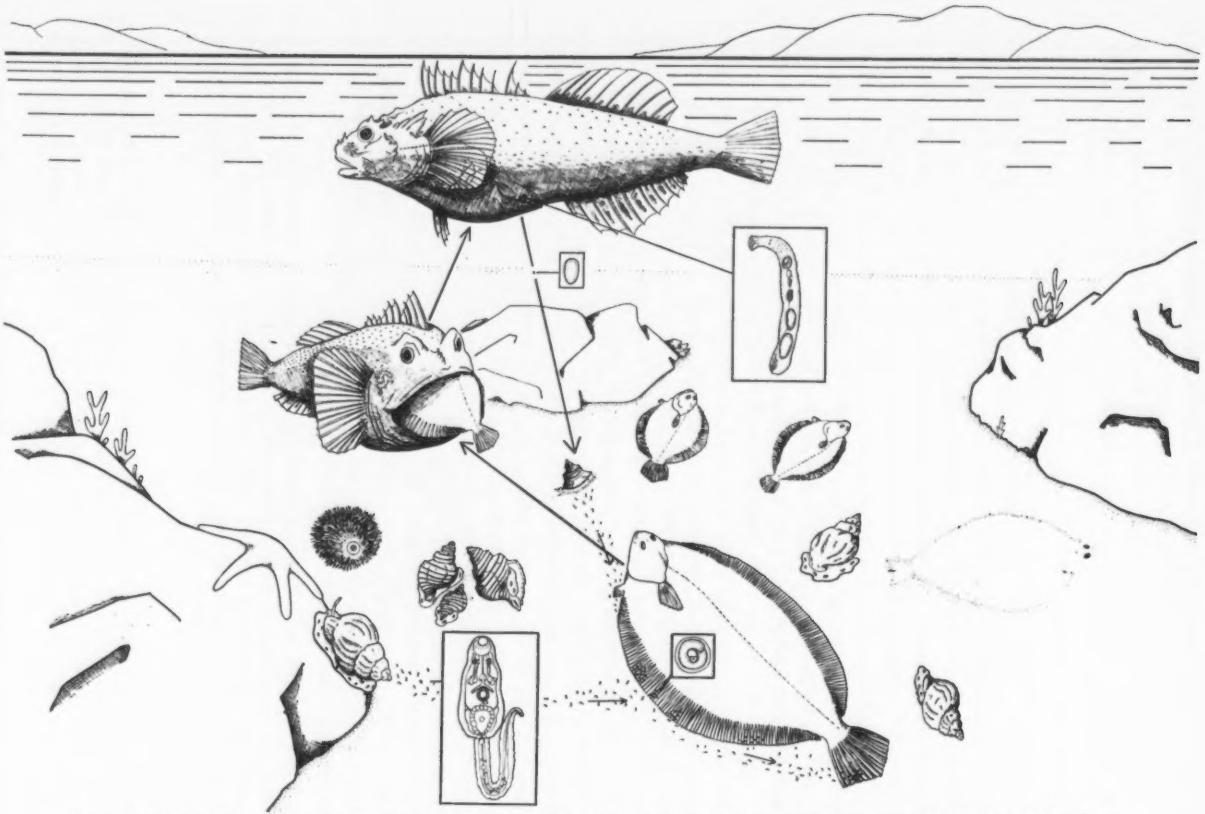

FIGURE 13. Pictorial representation of the life cycle of *S. baccatum* as it occurs in Passamaquoddy and St. Mary Bays.

Fundy the flounders appear in shoal waters near shore during the summer and early fall, moving off into adjacent deeper water in the winter and early spring. Hatching begins in the late spring and may continue during the early summer, with small fish of the year being collected in seine hauls along the shore, in coves and estuaries from August through October. The smaller fish of the most recent hatching and those two or three years of age remain during the entire year near the shore, moving off only slightly for the winter months. In general, the older fish disappear into deep water in November and December. After the second or third year the fish move into deeper waters and it is during this period that the greatest change in infection takes place. The characteristic of highly localized stocks is emphasized in the incidence of flounders in different localities. For instance, the infection incidence along the eastern shore of the bay is considerably higher than that along the western, except at the mouth of the St. Croix River (Joe's Point) where infection is very high, whereas it is very low at the head of the St. Croix. The S. *baccatum* infection then serves as an effective "tag" both for populations and for localized stocks of flounders within a population.

The offshore movement of larger and older fish coincides with the increase in infection in individual flounders of any area. Although the larger fish showed heavier infections than smaller ones, fish recovered in deep waters showed higher infection with metacercariae than did similar-sized fish inshore. This indicates deeper water to be the more important focus of infection.

The primary intermediate or snail hosts, *Buccinum undatum* and *Neptunea decemcostatum*, are common in Passamaquoddy Bay, the former more so than the latter. In discussing the snail host only *B. undatum* will be referred to, since no *N. decemcostatum* were found infected other than in the presence of *Buccinum. B. undatum* exists in Passamaquoddy Bay and in the Bay of Fundy as a separate variety which has been discussed by Yonge (1949). It differs from the same species elsewhere by its ability to extend into the littoral zone where it may be collected in colonies of *Mytilus edulis* L. and *Thias lapilla* L. It was never found infected, however, in areas which are not always covered by water of the tides of least amplitude. The only infected specimens collected just below the low water mark were taken on the minus ebb of spring tides. The snail is particularly fond of a rocky bottom, especially along the borders of open bottom, be it sand, hard mud or gravel. The colony usually extends for some distance into the covered "flat" adjoining the rocky area.

The sea raven, the definitive host, is the only abundant carnivorous fish in Passamaquoddy Bay anatomically equipped to handle fish larger than itself. It has large flexible jaws with multiple recurved teeth, and a big mouth equipped with patches of teeth both above and below. Its stomach was found to contain eelpouts up to twice its own length. The sea raven seizes moving prey and retires to dark clefts or ledges of rocks either when it is frightened or, frequently, when it has completed swallowing a meal. When collecting snails at low spring tides the author has often encountered this predator.

Because of the intimate nature of the association between hosts and because

of the problems involved in eliminating any one of the hosts of the life cycle of *S. baccatum,* control is impractical. The parasite does not hamper the growth rate of the flounder and the worm can neither harm man nor develop in him.

Although cysts are easily visible to the naked eye in fresh fillets, they are much less noticeable in frozen ones.

SUMMARY

The trematode, *Stephanostomum baccatum,* occurs in a number of marine teleosts from the Baltic Sea to the Bay of Fundy. Adult trematodes parasitize the recta of carnivorous teleosts and generally inhabit fish-eating cottids; metacercarial cysts are found in the superficial musculature and dermal surfaces of flat fish as well as in the gills and soft exposed parts of round fish.

Life history studies in Passamaquoddy Bay, N.B., show that the sea raven, *Hemitripterus americanus,* is the prevalent definitive host in inshore waters of the Bay of Fundy, the winter flounder is the flatfish most frequently parasitized by the metacercariae, and gastropods of the family Buccinidae serve as primary intermediate hosts in whose digestive gland and gonad are found the rediae from which escape the free-living cercariae which eventually penetrate the flounder. The distribution of the parasite in Canadian maritime waters roughly parallels the distribution of the snail hosts.

Studies of the winter flounder in the Bay of Fundy suggest that the parasitism in this flatfish is greater in deeper than in shallow inshore waters, that larger flounders bear heavier infections than do small ones, that the infection is not pathogenic, and that the parasitism of the flounder by the trematode does not follow any seasonal pattern.

The heterosomatic hosts vary in their degree of *Stephanostomum baccatum* parasitism but in general the inshore species, *Pseudopleuronectes americanus,* is more heavily parasitized than are any of the other species. Offshore species of flounders may be parasitized by the worm but are heavily infected only when taken in or near inshore waters. The heaviest infections of flatfish examined are found in St. Mary Bay, N.S., and in Passamaquoddy Bay, N.B.

No control of the parasite by breaking the life cycle is suggested.

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Sex Ratios in Sockeye Salmon (*Oncorhynchus nerka*)[1]

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ABSTRACT

A low male:female ratio (average for 14 years—32.4% males) occurs in the sockeye salmon spawning escapements to Cultus Lake. Factors likely to cause such unequal sex representation are examined. Sex ratios of seaward-migrating smolts (7 years' records) were found to approximate 50:50. Selection of male fish by the gill-net fishery, while contributing, does not appear great enough. Therefore, a greater mortality of male sockeye during the period of ocean residence seems indicated, and records for two series of data are presented.

INTRODUCTION

In the course of investigations conducted from 1925 to 1938 by the Fisheries Research Board of Canada at Cultus Lake, British Columbia, into the natural and artificial propagation of sockeye salmon (Foerster, 1936a, 1938; Foerster and Ricker, 1941) the program of operation required the complete enumeration of all adult sockeye reaching the counting weir in Sweltzer Creek, the outlet stream from Cultus Lake (Foerster, 1936a, figs. 2 and 3). The numbers of males and females counted each season are shown in Table I. Segregation into age-groups indicated that in most years, except those preceding the relatively "big" runs of 1927, 1931, 1935 and 1939, one age-group was dominant, the four-year one. In 1926, 1930, and 1938, large numbers of relatively small, precociously maturing three-year sockeye occurred, a size-group not heavily exploited by commercial gillnets. In 1927, 1933 and 1937, three-year-olds also occurred in appreciable numbers, seemingly heralding a greater than normal run the next season.

The disparity in the sex components of each season's run and the general relative preponderance of females, especially among the larger 4_2 and 5_3 fish, immediately attracted attention. Interest centred in the probable cause thereof, whether (*a*) an unequal sex ratio among young sockeye prior to migration to the ocean (*b*) a marked selectivity for male fish of the commercial gill-net fishery or (*c*) a more favourable survival rate for females in the ocean.

The problem of sex ratios in spawning populations, of how they are or might be altered by the commercial fishery, and what might be considered a suitable ratio of males and females to provide most effective fertilization of eggs deposited by spawning females, is an important one for management. Any superfluous escapement of male fish would represent a loss to the fishery and to full utilization of the resource.

SEX RATIO AMONG SEAWARD-MIGRATING SOCKEYE

For a number of years, samples of young sockeye migrating seaward from Cultus Lake were examined for sex as well as for size and age. Except for 1929

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TABLE I. Adult sockeye salmon counts at the Cultus Lake counting weir, 1925–1938. For the years 1925 to 1931 age separation was based on examination of scales from a sample of the run; from 1932–1938 age-groups were designated by numbers of marked or unmarked individuals observed at the weir.

Year	Age of males		Age of females		Total run	Ratio Male:Female	Percentage males among ages 4 + 5
	3_2	4 + 5	3_2	4 + 5			
1925	0	1,540	0	3,883	5,423	1: 2.52	28.4
1926	1,180	1,942	333	1,616	5,071	1: 0.63	54.6
1927	1,250	24,799	1,491	54,885	82,425	1: 2.16	31.1
1928	0	3,878	0	11,461	15,339	1: 2.96	25.3
1929	9	1,636	0	3,437	5,082	1: 2.09	32.2
1930	1,650	3,203	28	5,514	10,395	1: 1.14	36.7
1931	0	7,269	1	25,168	32,438	1: 3.46	22.4
1932	28	713	0	1,518	2,259	1: 2.05	32.0
1933	538	1,027	69	1,837	3,471	1: 1.22	35.8
1934	80	3,965	6	15,657	19,708	1: 3.87	20.2
1935	9	5,606	0	10,174	15,789	1: 1.81	35.5
1936	35	3,261	2	5,061	8,359	1: 1.54	39.2
1937	1,721	513	113	714	3,061	1: 0.37	41.8
1938	3,838	1,673	388	7,443	13,342	1: 1.42	18.3

and 1930, the samples were taken in specific ratios (1:50, 1:100, etc.) set up according to the anticipated size of the migration. In certain years the sample ratio was changed during the run, but for the present study the samples have been adjusted to conform to a single ratio for each year—the smallest one used. For 1929 and 1930 portions only of the samples, selected to give a seasonal representation, were sexed.

The data, shown in Table II, reveal that, for the seven years for which sex determinations of smolts were made, the overall male to female ratio is 1:0.998 which, tested by chi-square, indicates no significant departure from a 50:50 sex distribution. In one year only, 1930, do the numbers of males and females differ

TABLE II. Sex ratios of seaward-migrating sockeye salmon from Cultus Lake, as revealed by random samples taken throughout each season's run in a set ratio of 1: 100 or multiple thereof, except for 1929 and 1930.

Year	Number of males	Number of females	Ratio Male:Female	Chi-square	d.f.
1929	148	142	1: 0.96	0.124	1
1930[a]	170	241	1: 1.42	12.266	1
1932	1,871	1,838	1: 0.98	0.294	1
1933	799	740	1: 0.93	2.260	1
1934[a]	445	430	1: 0.97	0.460	1
1935[a]	598	661	1: 1.11	3.152	1
1937	786	755	1: 0.96	0.624	1
Totals	4,817	4,807	1: 0.998	0.005	1
Sum of chi-squares				19.180	7

[a]Two age-groups involved, as discussed below.

to a significant extent, the males being appreciably fewer than the females (1:1.42).

It is apparent, therefore, that differences in sex representation among the seaward-migrating young cannot be responsible for the marked dominance of females in the adult runs of most years. The close adherence to an even sex distribution among year-old sockeye smolts leaving Cultus Lake is paralleled by findings from Babine Lake in northern British Columbia (Dombroski, 1952) where 51 per cent of the 2,795 yearling smolts were males and 49 per cent females; and by recent examination of sockeye smolts from Lakelse Lake in 1952 where, of the 1,671 smolts sexed, the proportion–885 males and 786 females or 1 male:0.888 female–did not depart significantly from an even sex distribution. Barnaby (1944) reports for 3-year and 4-year red salmon (*O. nerka*) migrants at Karluk, Alaska, 50.18 and 50.09 percentage male representation, respectively, in the combined migrant samples, 1925–1934

VARIATION IN SEX RATIO WITHIN A MIGRATION

A. Between Age-Groups

In smolt seaward migrations from Cultus Lake two age-groups may occur, fish in their early second year (yearlings or age-group I) and those in their early third (two-year-olds or age-group II). These age-groups may have decidedly differing sex ratios and, when both are well represented in a smolt run, the pooled sex ratio may be influenced considerably in comparison with a year when age-group I predominates.

For example, for the smolt migration of 1930, Table II, which consisted of 38,600 I-year fish and 66,600 II-year fish, the breakdown of the sex distribution of the sample of 411 fish was as follows:

Age-group	*Total*	*Males*	*Females*	*Ratio*	*Chi-square*	d.f.
I	123	52	71	1:1.37	2.93	1
II	288	118	170	1:1.44	9.39	1
Total	411	170	241	1:1.42	12.27	1
Sum of individual chi-squares:					12.32	2

The significantly large excess of females in the more abundant II-year age-group was mainly responsible for the 1:1.42 ratio for the run as a whole. (The excess of females in the I-year sample was also considerable, but because of the small number of fish it was non-significant, and the nearly 1:1 ratios for yearlings in other years suggest that it is a sampling effect.)

In contrast, however, for the run of 1934, which consisted of 184,500 smolts (121,200 I-year and 63,300 II-year), the sample sex ratio breakdown was:

Age-group	*Total*	*Males*	*Females*	*Ratio*	*Chi-square*	d.f.
I	556	286	270	1:0.944	0.46	1
II	319	159	160	1:1.006	0.00	1
Total	875	445	430	1:0.966	0.26	1
Sum of individual chi-squares:					0.46	2

In this year there was no appreciable variation in sex ratio in either age-group and no significant variation from an even representation.

B. Within One Age-Group

In order to reveal in what respect the sex representation may vary within the season for a single age-group, the sample of 1541 smolts taken from the 1937 migration of 3,102,000 migrants (i.e., a sample of 1 to 2,000) has been analysed as follows:

Period	*Total sample*	*Males*	*Females*	*Ratio*	*Chi-square*	d.f.
To April 20	136	64	72	1:1.12	0.471	1
April 21-24	598	275	323	1:1.17	3.853	1
April 24-28	470	253	217	1:0.86	2.757	1
April 28 on	337	194	143	1:0.74	7.718	1
Total	1,541	786	755	1:0.96	0.624	1
Sum of individual chi-squares:					14.799	4

For the 1937 migration as a whole, the sex distribution did not exhibit a significant departure from a 50:50 representation. Samples taken throughout the run showed, however, slightly different sex ratios. That for April 21–24 differs significantly from 1:1 at the .05 level of probability, whereas that for April 28 to the end of the season is significant to the .01 level. The sum for all four periods is also above the 0.01 level. The data, therefore, indicate a relatively greater number of females in the first half of the migration and of males in the last half.

In 1935 a sample of 1,183 smolts taken from a migration of 242,500 I-year sockeye (ratio – 1:200) shows the following variation in sex distribution:

Period	*Total samples*	*Males*	*Females*	*Ratio*	*Chi-square*	d.f.
To April 27	320	139	181	1:1.30	5.5126	1
April 28-May 6	469	238	231	1:0.97	0.1044	1
May 7-29	394	185	209	1:1.13	1.4620	1
Total	1,183	562	621	1:1.10	2.9426	1
Sum of individual chi-squares:					7.0790	3

There is again an abundance of females in the early part of the season as in 1937, but no excess of males in the later period is indicated.

The 1935 sample of II-year smolts (76 from a run of 14,200) may be similarly divided:

Period	*Total samples*	*Males*	*Females*	*Ratio*	*Chi-square*	d.f.
To April 27	39	18	21	1:1.67	0.115	1
April 28-May 6	22	10	12	1:1.20	0.091	1
May 7-29	15	8	7	1:0.88	0.033	1
Total	76	36	40	1:1.11	0.105	1
Sum of individual chi-squares:					0.239	3

With so few fish in the sample no significant variations are found, but again females are slightly more numerous in the early period of the run.

SEX RATIOS IN SAMPLES FROM THE COMMERCIAL SOCKEYE SALMON CATCHES

Reference to reports of sampling of trap-caught sockeye in the Strait of Juan de Fuca (Clemens, 1938, table VII, p. 37), which fish are presumed to be chiefly bound for the Fraser River System, reveals an overall sex ratio of 50:50

with but slight variation yearly therefrom. Salmon traps are considered to be generally a non-selective type of fishing gear. The sex ratios from trap-caught sockeye would suggest therefore that as the fish come in from the ocean the sexes are relatively uniformly represented.

Peterson (1954), from a quite intensive study of the selective action of gill-nets on Fraser River sockeye salmon, has intimated:

(1) that, while the mesh sizes used on the Fraser vary from about 5¼– to 6½–inch mesh, stretched measure, the most popular sizes range from 5¾– to 6–inch (p. 2);

(2) that small-mesh nets take predominantly small fish and the large meshes catch mainly large fish, and that, since, within any age-group, the large fish are mostly males and the small fish predominantly female, a definite selective action by mesh size occurs for sex as well as size of the sockeye (p. 44); and

(3) that spawning ground sampling for prevailing sex ratios reveals, in general, appreciably fewer males than females (p. 90, table XLII).

There appears to be, therefore, clear evidence that the Fraser River gill-net fishery can be quite selective with regard to both size and sex of sockeye and may cause, consequently, an unequal sex ratio in the spawning areas such as Cultus Lake. Interesting comparisons are made of the drop in average length and rise in percentage of net-marked sockeye examined at Hell's Gate when gill-net fishing takes place in the lower Fraser (p. 61, Fig. 21) and on the relation of the periods of gill-net catches in the river estuary to the dipnet catch and average length of sockeye at Farwell Canyon (p. 72, Fig. 72).

However, for the Cultus Lake sockeye which have been found (Foerster, 1936b) to pass through the Fraser River gill-net areas relatively late in the season, September to November, it may be noted (p. 92, table XLIV) that, in those years (1950 and 1952) when fishing was prohibited or restricted only to the use of 8–inch and larger meshes for most of the autumn period or curtailed for a portion of the period (1946, 1947, 1949), the percentage of males observed at the Cultus Lake weir (p. 90, table XLII) was not too greatly different from those years when full season fishing was permitted (1945, 1948, 1951). The records shown by Peterson are of later years than those given in Table I above. They would seem to indicate that, irrespective of the extent of the gill-net fishery during the season and any selectivity for male fish, there are fewer males than females in the Cultus Lake sockeye salmon population coming in from the ocean.

Cultus Lake Marked-Sockeye Returns

More pertinent, perhaps, to the consideration of the sex ratios in a specific sockeye population in the ocean and the effect of fishing gear on sex selectivity, are the records obtained for Cultus Lake marked sockeye adults returning from two marking experiments conducted in 1930 and 1931 (Foerster, 1936b). The recoveries were as shown in Table III.

The Fraser River gill-net fishery did remove a greater number of 4_2 and 5_3 males than females in each of the years, in contrast to the trap and seine fisheries

TABLE III. Recoveries made in the fishing areas and at Cultus Lake of marked adult sockeye resulting from the marking of seaward-migrating sockeye smolts at Cultus Lake in 1930 and 1931.

	1930 experiment						1931 experiment					
Recovery year	1931		1932		1933		1932		1933		1934	
	3_2		$4_2 + 5_3$		5_2		3_2		$4_2 + 5_3$		5_2	
Recovery area	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
U.S. traps and seines	*a*	*a*	436	695	11	2	12	0	3,215	4,047	159	99
Fraser River	*a*	*a*	480	339	12	11	1	0	1,038	772	125	15
Cultus Lake	18	10	465	1,334	3	5	28	0	1,022	1,834	127	149
Totals	18	10	1,381	2,368	26	18	41	0	5,275	6,653	411	263

[a]No search made.

which are considered to be practically non-selective. When the Cultus Lake spawning-escapement counts are studied, however, it becomes apparent that the sexes could not have been evenly represented initially, certainly not in the 1932 run. Not all the sex disparity in 1932, and even less in 1933, could have been due to commercial gill-net selectivity.

SURVIVAL DURING OCEAN RESIDENCE

The only evidence now available which might give a comparison of degree of survival of male and female sockeye during the period of ocean residence is that presented for the Cultus Lake populations of 1932 and 1933—populations which were marked, by removal of fins, at the time they migrated to sea in the spring of 1930. In 1930 a sex ratio of 1:1.42 was observed among the sample of seaward-migrating smolts (Table II). For the returning marked adults in the fishery and escapement (Table III) in the 1930 experiment the sex ratio was 1:1.68. There seems to be no reason to believe that the effect of marking the young smolts would be any more severe and lead to heavier mortality among males than females; nor should there have been any bias favouring recovery of more marked females than males in the fishing areas. There is the suggestion, therefore, that a greater mortality occurs among males during the period of ocean residence, than among females. Support for this suggestion is given by the return of marked adults of the 1931 experiment. A sex analysis of the smolts of 1931 was not made but, assuming it to have been similar to other migrations (Table II) except 1930, hence approximately 1:1, the return of marked adults (Table III) in 1933–34 with a sex ratio of 1:1.21 (or 0.83:1) indicates a disappearance, somewhere, of approximately 17 per cent of the probable number of male fish. The indicated selectivity of the gill-net fishery on the Fraser River (Table III) is not sufficient to accomplish this.

Barnaby (1944) has reported a change in sex ratio between seaward migrants and returning adults—from 50 per cent males and 50 per cent females to 44 per cent males and 56 per cent females—which could not be accounted for by a small gill-net fishery. He remarks that "a differential mortality in favour of the females during the time spent in the ocean does not appear probable. A satisfactory explanation of this phenomenon is lacking at the present time." These further Cultus Lake data add weight to the probability of a greater mortality among males in the ocean.

DISCUSSION

The several years' data from Cultus Lake (Table II) confirm the general understanding that upon migration to the sea the young of the sockeye have generally an even sex distribution.

That this condition may not prevail throughout the period of ocean residence is suggested by some of the data. Analysis of commercial salmon trap catch samples (Clemens, 1938), where gear which should not be selective as to sex of fish is used, suggests a fairly even sex ratio in the incoming adult sockeye runs,

but the findings for one specific population (the "marked" Cultus Lake runs of 1932 and 1933, Table III) are at variance.

Attainment of maturity at different ages tends to complicate the situation. If it were a fact that among ocean-resident sockeye the sexes were equally represented and if, as has already been instanced for Cultus Lake (Table I) and as occurs for other sockeye salmon areas, a proportion of the male fish, which mature normally in their fourth year, do so precociously in their third year and return to the rivers for spawning, a surplus of females should be left in the ocean for return to the river in the following year. The same situation would apply among normally maturing five-year sockeye, if some of the males matured precociously in their fourth year. Precocious maturing and spawning of male fish may, consequently, tend, to a certain degree, to bring about a surplus of females in the succeeding season. The fact remains, however, for Cultus Lake (Table I) and other Fraser River areas (International Pacific Salmon Fisheries Commission Annual Reports, 1943–54), that among year-classes which have no important number of precocious males in the run, the preponderance of females continues. The Cultus Lake records of "marked" adult recoveries in the fishery and the escapement, when separated (Table III) into the 4_2 and 5_3 (1+ years of ocean residence) and 5_2 (2+ years of ocean residence) age categories, show no preponderance of females in the latter (5_2) group, such as would occur if a precocious return of normally 5_2 males in their fourth year were to leave a surplus of females for the succeeding season. In fact the 5_2 fish included a considerable excess of males.

The commercial gill-net fishery can be selective for males, particularly toward the end of the season when the fish are maturing and developing the secondary sexual characters of hooked nose and humped back, as shown by Peterson (1954) for sockeye salmon runs to the Fraser River. The three years' records pertaining to the commercial fishing for marked Cultus Lake sockeye in 1932, 1933 and 1934 confirm this, but do not wholly account for the great disparity in the sexes when the fish arrive at the Cultus Lake counting weir. An Indian gill-net fishery in the Fraser above the commercial fishing area may be particularly selective for males, but this is a minor fishery and the removal of male fish would not be great enough to account for the heavy minority of males escaping to the spawning grounds in most years.

It has been suggested by some investigators that a greater exploitation of salmon stocks can be achieved, without unfavourable effect on seeding, by capturing a greater proportion of male salmon. This practice may be applicable to certain waters where an even sex ratio prevails or where male fish predominate. Reference to data for the spawning runs to up-river areas of the Fraser (International Pacific Salmon Commission, 1941–1953 and Peterson, 1954) reveals that in many of the heavy-spawning populations the female fish already predominate. Records for the Babine Lake area, the principal spawning ground of the Skeena River system (Aro, 1952, Table II), also show a dominance of females in the spawning run, if three-year-old males ("jacks") are ignored. Thus disparity in the sexes of normal-sized fish is found, despite the greater

number of females noted in the commercial fishery samples (Foskett, 1953, Table XII). Therefore, a substantially greater removal of males by the fishery might have serious consequences in reproduction and in maintenance of the populations at high levels.

SUMMARY

In the spawning escapements of sockeye salmon to Cultus Lake, 1925 to 1938, it was observed that female fish generally predominated, in some years quite heavily. Sex ratio analysis of samples taken from six seaward-migrating populations of young sockeye from Cultus Lake, 1929–1937, showed an overall 1:0.998 male to female representation. In one year only did a significant difference between the sexes occur, this because of a heavy population of II-year smolts in which females predominated.

Examinations of available data on the sex ratios of sockeye taken by the commercial gill-net fishery indicated a certain degree of net selectivity for males, particularly for the late-running populations when the developing secondary sexual characters make them more vulnerable to the gill-nets. A small gill-net fishery by Indians in the Fraser River above the commercial fishing boundaries may also remove a greater proportion of male fish than females.

Such selectivity of male fish by the gill-net fishing gear does not seem to account, however, for the preponderance of female fish in the spawning escapements to Cultus Lake. Therefore data pertaining to the return of marked adult sockeye from smolt marking experiments conducted in 1930 and 1931 were examined. They suggest that greater mortality of male fish may occur during the period of ocean residence. Sex proportions for the smolt run of 1930 were 1:1.42. Among returning adults the proportions were 1:1.68. For the 1931 experiment where the sex ratio of smolts was probably 1:1, in conformity with other years when the bulk of the migrants were of age-group I, the adult return was found to represent a 1:1.21 male to female sex ratio. For Alaska sockeye salmon (Barnaby, 1944) a similar change in sex ratio between seaward migrant and adult stages was found.

It is suggested that further evidence is desirable before any procedure aimed at a substantially greater removal of male fish by the commercial fishery is applied widely. The data available suggest that, in general, male fish on the spawning grounds are less abundant than females.

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